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THE PHYSIOLOGY OF INCOMPATIBILITIES¹

A. B. STOUT

In general survey, physiological incompatibilities in fertilizations include two groups of phenomena:

1st. There are the very general and characteristic failures of cross-fertilization *between* different species, long considered as the most adequate evidence of specific distinction; and

2d. There are those physiological limitations to free and general fertilization *within* species exhibited best in the failure of certain homomorphic hermaphrodites to self-fertilize, but also in the cross-incompatibilities among seed-grown individuals of the same species or race.

Certain aspects of the physiology of these incompatibilities are clear. They exist and are in operation when the sex organs and sex elements are in a condition for proper fertilization; the elements do not function in certain relations but do in others; fertilization is discriminative.

It is not, therefore, a question of what brings the spores or gametes to ripening, or of the mere production of those egg or stylar secretions or chemotactic influences which make fertilization possible. It is rather a question of a very special kind of development or physiological condition which discriminates between fertilizations when they are otherwise possible.

Inter-specific incompatibilities are very generally considered to involve species specificity. They are expressed in the interaction between egg secretions and sperms, in mechanical and chemical resistance of the cortical layers of eggs to the entrance of sperms, in the extrusion of sperm chromatin after fertilization, in the death of the heterogenetic hybrid, or in the sexual impotence of such hybrids. In all these ranges of expression the incompatibilities appear to be deep-seated and inherent in the physical and chemical differences in the organization of species.

Turning now to intra-specific incompatibilities, there is apparently a very different physical basis. Here there is self-incompatibility involving the germ cells of a single individual. Here also there is cross-incompatibility between individuals of the same parentage. Such cases are frequent among homomorphic hermaphrodites. They are so widely distributed in the families of flowering plants that it would seem that there must be some

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fundamental principle operating in their origin and development. In these higher plants there is the development of a nearly naked egg (free of a decided membrane) imbedded in the tissue of the ovule, and a highly specialized male gametophyte—the pollen tube—with its various growth relations in the style. While fertilization in these cases involves a series of physical and chemical relations, it is fundamentally an egg-and-sperm reaction.

It is to be noted that studies of the physiology of pollen germination have failed to reveal a specificity that is comparable or related to the compatibility or incompatibility found in homomorphic species. It has, however, long been known that in cases of self-incompatibility the pollen tubes often make feeble growth in the style, and more recently it has been shown that their rate of growth is not accelerated as the eggs are approached. This condition apparently persists when incompatible pollen is mixed with compatible pollen and the tubes of both grow side by side in the style. This indicates that the reactions are decidedly discriminative and suggests that they involve reactions of the pollen tubes to secretions of the eggs. There is, however, evidence that in many grades of self-incompatibility the injurious effects may be exhibited after what is apparently a successful fertilization.

One aspect of the development of self-incompatibility in the hermaphrodite is clear. Every such individual is itself the result of a compatible fertilization in which two cells fused, and the two elements of the resulting diploid organization show themselves compatible throughout the somatic life of the individual; but the two kinds of sex elements produced by it are incompatible, and this is of course irrespective of their germ-plasm complex. The incompatibility arises along with sex differentiation, which in seed plants begins with the development of pistils and stamens and is independent of any readjustments of the germ plasm in the reduction divisions.

The biogenetic nature of the development of self-incompatibilities is further indicated by the wide variations which exist in their expression in individuals. Between the extreme or alternative conditions there are many intergradations, and the extreme conditions are reversible in a progeny. This is the general rule of behavior in such pedigreed cultures as have been critically tested in this particular. Cross-incompatibilities exhibit quite the same ranges of expression, and here reciprocals may give directly opposite results.

But there is also conclusive evidence in certain species of cyclic changes in the self-compatibility of an individual. These are best seen in plants which have a somewhat extended and continuous period of bloom. In some species there is self-compatibility at the end of the period of bloom; in others the climax of self-compatibility is at the mid-period of the bloom, and for certain perennials there is some evidence of changes from year to year in relation to the age of the plant. It is to be noted that a mid-period

self-compatibility is preceded and followed by self-incompatibility. There is alternative expression of extreme grades of compatibility and incompatibility in the series of flowers produced in succession on the same branch. The functions of fertilization are in such cases operating in a cycle of intensities.

It may here be reported that, in the species *Brassica pekinensis*, self-incompatibility of a plant as a whole or of a family of plants may be decidedly changed by a cultural treatment which reduces vegetative vigor. In a family of this species grown for three generations, less than 10 percent of the total of 326 plants were highly self-compatible and there was no hereditary effect of selection for self-compatibility. When a generation of this family was grown in small pots with decided reduction of vegetative vigor, of a total of 1,128 plants there were 734 (65%) that were highly self-compatible, and only 22 (less than 2%) were self-incompatible. Furthermore, a large proportion of the former were self-compatible in the earliest flowers that opened. The family was decidedly changed in regard to the number of plants that were self-compatible, and in the individuals the characteristic cycle was altered. Such results, together with the other behavior noted above, indicate that there is a direct and very decided physiological correlation between vegetative vigor and the functional properties of the organs concerned with fertilization.

This is at least suggestive that the physiological conditions which restrict and limit indiscriminate fertilization within species are not only subject to internal regulation, but that in some cases at least they are correlated with changes in vegetative vigor.

The situation gives hope that the cyclic expression of sexual affinities and the development of extremes of compatibility may be so regulated experimentally that the specific biogenetic factors and conditions operating in this highly specialized differentiation may be determined.

NEW YORK BOTANICAL GARDEN

POLLEN- AND SEED-STERILITY IN HYBRIDS¹

BRADLEY MOORE DAVIS

Sterility of hybrids in various forms and degrees is a phenomenon so frequently presented to the plant breeder and geneticist that in some form and in some degree it is rather to be expected. The first problem in its study demands a critical examination to determine in the life history the place of those conditions that bring about the sterility in question. In earlier days the gametes were generally expected to carry the blame of failure to reproduce the line. More recent studies have shown that responsibilities for sterility cannot be so easily placed.

Sterility, as expressed by varying proportions of abortive pollen and abortive ovules, is very common, and since it is easily recognized this manifestation of sterility has received the greatest share of attention. It is expressed by failure of the pollen grain to attain full size, the structure shriveling and usually losing its protoplasmic contents. In a like manner, the megaspore or embryo sac does not reach a normal development in the ovule. Such behavior results in failure to produce gametes, and cytological studies, as far as they have gone, indicate that this form of sterility, at least frequently, has its causation in irregularities of the reduction divisions which immediately precede the differentiation of micro- and megaspores.

During these mitoses spindles may not be normal in form, chromosomes may be distributed in varying and irregular numbers, and the preparations for the reduction divisions may show abnormalities. Such phenomena clearly indicate a breakdown in the mechanism of nuclear division at this critical stage in the life history. It seems reasonable to assume in these cases that the hybrid must carry a germ plasm the structural elements of which can not conduct themselves in the orderly manner so characteristic of meiosis. Speculation on the reasons for the obvious breakdown of the cell and nuclear mechanism at this point in the life history would lead us too far afield for the purposes of this paper. It seems clear, however, that the causes lie in the heterozygous nature of the germ plasm, since we do not find this form of sterility in pure material. Abnormalities of chromosome distribution are clearly invited when the two sets are of different genetical constitution, since irregularities of segregation are rendered much more likely.

It should not be assumed, however, that the presence of abortive pollen and abortive ovules is proof positive that the parent plant is hybrid, although

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any plant showing high proportions of shriveled pollen may very justly be an object of suspicion. There is a form of pollen sterility due to malnutrition, and this condition may be brought on experimentally by operations seriously affecting the vegetative activities of a plant, as, for example, stripping the leaves from stems. In this connection should be mentioned a form of abortion presented in heterosporous plants when one or more megaspores, perhaps through more favorable position or the good fortune of a better start, are able to develop at the expense of their neighbors which, giving up their substance, are sacrificed for the good of those megaspores that survive. This is fundamentally a form of sterility due to malnutrition, but it is not of course peculiar to hybrids.

Sterility which results from failure to develop gametes is one thing, and sterility due to the inability of gametes to unite is quite another. The latter form of sterility is much more difficult of study in plant material than in animal because the fusion of gametes in higher plants takes place in structures and tissues difficult of examination. Zoölogists recognize the phenomenon and it may be expected to be present in plants, but forms most profitable for study seem rather more likely to be found in groups of the thallophytes than among the higher plants. Sterility of this character need not be due to particular physical or chemical conditions that prevent the union of gamete protoplasts. Pollen grains may not find the secretions of the stigma favorable for their germination. There is probably a very large amount of sterility which results from the inability or slowness of some pollen tubes to penetrate certain lengths of style. We know something of this matter through the studies of East on *Nicotiana*, of D. F. Jones with pollen mixtures in maize, and from observations of Buchholz and Blakeslee on pollen-tube growth in *Datura*. It is probably a factor of importance in determining some of the results of *Oenothera* breeding.

Zygotic sterility is very common among plant hybrids. It means that the zygote is either unable to develop at all or that it produces an embryo which dies early in the production of a seed-like structure. In either case this form of sterility may be suspected from the presence of shriveled ovules or shriveled seed-like structures of various sizes, but generally smaller than normal seeds. Sometimes there may be structures as large as seeds and externally like them but without embryos. Zygotic sterility is therefore conveniently recognized by seed sterility, only care must be taken to make sure that seeds are really sterile because of internal conditions and not merely slow of germination. In plant genetics it is necessary to know these facts before conclusions can be drawn on the significance of so-called "percentages of germination." Conditions must be arranged to force seeds to complete germination, and examinations of the residue of ungerminated seed-like structures must be made to make sure that germination is really complete.

Of course it is impossible to draw a fast line between the embryo which dies in the seed and the embryo which comes forth a weakling unable to

live long as a seedling. The geneticist working in certain groups knows this latter type of seedling very well. *Oenothera* material is full of illustrations. One type is that of a seedling which expands green cotyledons but the hypocotyl is totally unable to develop a root. Other forms are delicate, frequently etiolated seedlings which live only a few days even when nursed along with most particular attention to their needs of suitable soil, careful watering, and cooler temperatures. Perhaps some of these seedlings are accidents of development, but it is clear from many studies that there are large groups in which the inability to develop rests on a genetical basis and is really the expression of a degree and form of sterility.

Thus, from forms of zygotic sterility expressed by abortive embryos in seed-like structures, we pass insensibly to conditions illustrated by classes of weak seedlings which make a start only to die sooner or later. This is truly a form of sterility when the behavior is due to the germinal constitution of the seedling, and it is impossible to draw lines sharply in the wide range expressed by the various degrees of impotence. Examples of this form of sterility are well known to every plant geneticist who follows carefully the fate of seedlings from hybrid material when germination is complete. It not infrequently happens that large groups of etiolated seedlings appear, or weak dwarfs of various forms, or plants which make considerable growth but fail to mature. Most of these products die early even with the best of care; very few will live under the conditions of the open garden.

In the foregoing sketch I have endeavored to make clear the fact that sterility in plants is expressed in a number of very different forms and may operate at several points in the life history. The fact that the life history of plants is made up of two generations, gametophyte and sporophyte, with the three critical periods of chromosome segregation, fertilization, and embryo development frequently associated with involved physiological and histological conditions adds greatly to the complications of observation and interpretation and makes the study of sterility in plants more difficult than that of animals.

With so many forms of sterility known and expressed in such various ways, the specific causes must be very numerous. Some of them may be relatively simple, as when pollen fails to function because of delay in germination or slowness of tube growth. Even a breakdown at the time of the reduction divisions may be something of an accident when due to chance irregularities of chromosome distribution. On the other hand, sterility based on inability of two sorts of germ plasma to work in harmony, whether in the beginning or at the end of a life history, presents problems that are difficult to vision.

The geneticist postulates, as a form of expression, lethal factors in expressing results of his experimental work when sterility appears, and his formulae are of course justified as steps towards an understanding of finalities. The lethals of the geneticist are placed as genes in the chromo-

somes, and it must be confessed that we cannot show any reasons why they may not be there even though their presence adds mightily to the responsibilities of these heavily worked cell structures. We cannot say that slowness of germination on the part of a pollen grain may not be due to the character of substance or lack of substance in some region of a chromosome even though the pollen tube grows through activity of the ectoplast. On the other hand it may be that some lethals are present outside of nuclear structures. Breeding studies should be able to separate cytoplasmic lethals, if such exist, from those that are associated with chromosomes, since the two would be expected to follow different systems in inheritance.

We have treated sterility as though it depended in the last analysis on factors internal to the organism which may be postulated as genes and which express themselves through inheritance. With respect to sterility in hybrids, its association with germ-plasm organization is generally evident. It is a fair question to ask whether sterility ever has a basis other than that of germ-plasm organization. The temptation is sometimes great to lay the responsibilities of sterility to causes outside the organism and thus to separate a sort of physiological sterility from that which has a genetical relation. There are, for example, forms of sterility brought out by disease or by physiological conditions harmful to the plant. Supposing such sterility to be only partial, as is frequently the case, we should not of course expect the inheritance of this acquired sterility for the same reasons that we do not expect the inheritance of an acquired morphological character. So far as I am aware there are no reasons to regard sterility as other than a characteristic dependent upon germ-plasm organization and dependent in the same sense as are morphological characters.

As stated at the beginning of this paper, hybrid material is generally expected to exhibit in some degree sterility of various sorts. Hybrid material is also generally expected to show its heterozygous nature in breeding by throwing a varied assortment of forms in its progeny. There is coming to be recognized, however, a type of hybrid that reproduces itself perfectly, throwing at most only occasional variants. Such hybrids satisfy fully our concept of a species as a kind of animal or plant which breeds true. They are *impure* species because their germ plasm in the diploid condition carries different sets of genes affecting characters other than those of sex. The *pure* species in contrast has a germ plasm carrying two similar sets of genes each contributed by one of the parents and each with the same genetical constitution except when genes responsible for sex and sex-linked characters are concerned.

Because the impure or hybrid species is of particular interest in relation to the problems of hybrid sterility I must discuss certain phases of this subject although they have been treated with some fullness in my earlier paper "Species, pure and impure."²

² Davis, B. M. Species, pure and impure. Sci., n. ser. 55: 108-114. 1922.

The impure species, although hybrid in its germinal constitution, breeds true because only such gametes unite and give progeny as will reproduce the heterozygous constitution of the parent plant. Other types of gametes to be expected from the segregation divisions of meiosis either do not develop or fail to function for one of various possible reasons, or, if they do unite, the zygote either can not develop at all or it produces an embryo or seedling which can not mature. In short, there are breakdowns at one or more of various critical points in the life history, and thus some form of sterility eliminates the development of all or nearly all groups of segregates possible to the hybrid in question, and only such combinations of gametes are effective as will give the genotype of the parent.

This concept of the pure-breeding hybrid is not a fancy. We have excellent evidence that impure species are common in the genus *Oenothera* and that *Oenothera Lamarckiana* is one of them. Certain lines of *Drosophila* are known to be impure, and we owe to studies of Muller on such material the theory of balanced lethals which offers the best notion of a mechanism in heredity responsible for the generally true breeding of an impure species and for the appearance of occasional variants which some geneticists call mutants but which are really segregates from the heterozygous stock.

The theory of balanced lethals postulates the presence of two different lethals, for example x and y , the first in one chromosome and the second in the other chromosome of a synaptic pair. The organism is therefore heterozygous for each lethal. The theory also assumes that each lethal is effective only in double dose. The reduction divisions in such material will give two classes of sperms and two classes of eggs, each class distinguished by the presence of one of the two lethals. Thus there will be sperms x and y and eggs x and y and the chance mating of these will give zygotes in the following proportions $1xx : 2xy : 1yy$. Zygotes xx and yy , because they have lethals in double dose cannot develop progeny, but the zygotes with the heterozygous combination xy will live and reproduce the impure or hybrid parent type. Thus an impure species or race will breed true and maintain a constant state of hybridism unless the relative position of the lethals is changed by a crossover or unless a lethal becomes ineffective through a mutation. A crossover makes possible a class of zygotes free from both lethals, because sperms and eggs would be of the two classes xy and oo and the zygotes would be in the proportions $1xxyy : 2xy : 1oo$. Through the class of segregates free from both lethals recessive characters would appear if genes responsible for their suppression were removed by way of the class homozygous for both lethals. The appearance of such recessives will simulate mutations although in reality they are manifestations of a process of segregation.

There is not time to carry farther a discussion of the bearing of the theory of lethals on the facts of hybrid sterility. It is not probable that conditions in *Oenothera* and *Drosophila*, two groups which have received

exceptional attention, are marked exceptions among animals and plants. Intensive studies on other forms are more than likely greatly to extend our recognition of the presence in nature of impure lines and impure species. Hybridization in itself probably invites the development of lethals in proportion as the mixing of diverse germ plasms disturbs delicate and vital adjustments and creates confusion in orderly processes of development.

The subject of lethals and impure species has come to have particular interest for the student of certain groups of plants which are conspicuous components of floras. The systematics of *Oenothera* has reached a stage so complex that much material can not be identified in the field and species may be determined only when their behavior is studied in the experimental garden. Systematic studies on violets and brambles have employed similar methods of genetical analysis, and many other groups will require the same sort of treatment. Then there are those large assemblages characterized by high degrees of self-sterility, conditions probably not uncommon in the Compositae. Here the progeny is always or usually cross-bred as in all unisexual animals and plants. Again, even when self-fertilization is possible, it has been found in some material that inbred lines are not so vigorous as the outbred and thus conditions favor hybridity.

We open a paper with a discussion of pollen- and seed-sterility in hybrids. We are led at the end to touch upon some of the most complex problems of genetics and taxonomy.

UNIVERSITY OF MICHIGAN

GENETICAL ASPECTS OF SELF- AND CROSS-STERILITY¹

E. M. EAST

With the exception of the war period, the genetical and physiological aspects of self-sterility in plants have been under investigation at the Bussey Institution of Harvard University for the last twelve years; and, as often is the case with material worked intensively, the experiments have opened up so many new problems that they will probably be continued for several more years to come. The opportunity afforded by this symposium for bringing together a summary account of that phase of the work having to do with heredity is very welcome, therefore, both because results as yet unpublished have thrown new light on the subject, and because the previous accounts have been too long and detailed for ready reference. The experiments to be reported on here include only those upon the genus *Nicotiana* which for the last three years have been carried on by Dr. E. S. Anderson, who gives me permission to refer to his unpublished records. Experiments on some other species which I started four years ago are not yet ready for publication; but it may be stated that the data from these later experiments are in no wise contradictory to what I shall have to say.

The self-sterile species used were *Nicotiana alata* Lk. and Otto var. *grandiflora* Comes, *Nicotiana angustifolia* R. and P. var. *crispa* Cav., *Nicotiana commulata* Fisch. and Meyer, *Nicotiana glutinosa* L., and a species believed to be *Nicotiana Forgetiana* (Hort.) Sand. A self-fertile species, *Nicotiana Langsdorffii* L., was also utilized.

Both *N. Forgetiana* and *N. alata* cross easily with *N. Langsdorffii*. The F_1 plants show no evidence of true sterility, *i.e.*, they form normal capsules full of seeds as readily as do either of the parent species. All F_1 plants are self-fertile; and when selfed produce F_2 populations consisting of about 3 self-fertile plants to 1 self-sterile plant. One may assume, therefore, that self-sterility in *Nicotiana* is due to the presence of the allelomorph of a dominant self-fertility factor, F . When a population is homozygous or heterozygous for factor F , it is self-fertile; when a population is homozygous for f , that is to say when it is ff , it is self-sterile. These results corroborate those of Compton for *Reseda odorata*, and have been strengthened by another similar investigation made by Baur on *Antirrhinum*.

The other three self-sterile *Nicotianas* used in the work, *N. angustifolia*, *N. commulata*, and *N. glutinosa*, will not cross readily with self-fertile species, hence the genetic relationship could not be determined. But from

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certain evidence gleaned from studying the behavior of the self-sterile plants among themselves, one is led to the belief that either the primary self-sterility factor exists in various allelomorphic forms each having a different efficacy in causing self-sterility or that secondary factors exist which modify this efficacy.

This variation in the efficiency of the self-sterility factor is a peculiar thing. It does not mean that all plants homozygous for *ff* are not self-sterile, for this is not the case. It means only that there is a considerable variation in the ease or difficulty with which environmental changes can produce the slight indication of self-fertility which I have termed pseudo-fertility. Under normal conditions all plants of these species are wholly self-sterile. When grown with ordinary care either in the greenhouse or out of doors they produce not a single seed after selfing, for the first month or so of the flowering season. Later, a few seeds will sometimes be produced after selfing, and this pseudo-fertility appears as a response to changed environmental conditions more readily in some families than others.

There has been some criticism of the use of the term *pseudo-fertility*. The critics would have it that a plant which produces any seed whatsoever after a self-pollination is self-fertile, no matter if it has shown complete self-sterility in 200 or 300 attempts at selfing under what I term normal conditions. The position of these critics is indefensible. It shows an astonishing ignorance of both genetical methods and genetical results. Furthermore, those who take this position are so handicapped by it that they can make no constructive analysis either of their own or other results on self-sterility, although the data yield to a very simple interpretation when it is understood that this pseudo-fertility is a mere environmental fluctuation having nothing to do with heredity. I might say in passing that every somatic character is affected by external conditions. In ordinary cases, such as flower color, one finds that he must make his records before the flower wilts and fades. In less common examples, like the *Drosophila* mutant having 12 legs, the individuals must be raised under extraordinary conditions in order to bring out the character—in this case extreme cold is necessary. Another example would be hair characters in the human race. Would these critics say that hair color could not be studied because a man becomes bald? Could it be maintained that I did not inherit brown hair, just because I do not have much of it left now, or because of the prospect that I will not have any left a little later? I propose to sit tight on this proposition against all-comers as a matter of honor.

Speaking seriously, pseudo-fertility in the self-sterile plants with which I have been working is a rare occurrence; but it may be caused by any proper combination of circumstances which tends to make the flowers hang to their stems longer and which tends to make the pollen tubes grow more rapidly. Concretely, it is found when the plants are old and the temperature is between 80° and 90° F.; but these conditions produce more marked

effects on some families than on others. Since there is no difficulty in distinguishing true self-fertility from pseudo-fertility, the phenomenon has its advantages. By pollinating young buds of old plants under proper temperature conditions, one can obtain selfed capsules containing between one tenth and one half of the normal complement of seeds, and thus one can deal with populations produced by self-fertilization in self-sterile strains.

The most interesting problem of self-sterility is the behavior of self-sterile plants when crossed among themselves. Darwin supposed each plant to be so specialized in its reproductive organs that, though it could not be fertilized by its own pollen, it could be fertilized by the pollen of any other plant of the same species. Such a particularized specialization he found difficult to explain. Fortunately it is not necessary to explain it, for it is not what actually happens. The self-sterile strains are made up of groups of plants wherein each individual is cross-sterile with all other plants of the same class and cross-fertile with all plants belonging to any other class. In other words, if plant *A* is sterile with plant *B* and with plant *C*, it may be predicted that plant *B* will be sterile with plant *C*; and if plant *A* is fertile with plant *X* which in turn is sterile with plant *Y* and plant *Z*, then it may be predicted that plant *A* will be fertile with plant *Y* and plant *Z*. I shall not discuss the physiological implications of this peculiar phenomenon, but shall describe briefly the facts emerging from the pedigree-culture experiments.

Perhaps the most important genetic question is whether these classes of plants, wherein the individuals are all sterile with each other, are classes which are analogous to the classes of purples, magentas, reds, pinks, and so on, found in the F_2 generation after a white sweet pea is crossed with a purple sweet pea. That is to say, it is desirable to know whether one is dealing with a case of straight inheritance comparable with other cases of inheritance, but where the members of the classes, instead of being distinguishable by visual methods, can be ticketed and grouped only by the criterion of cross-sterility.

To determine this, a population of plants from a cross between *N. Forgeiana* and *N. alata* was tested for cross-sterility. Only 2.4 percent of cross-sterility was found, a percentage so small that it is not difficult to see how easy it was for Darwin to be misled into thinking that every plant within a self-sterile species was cross-fertile with every other plant. Though computation shows that from 20 to 25 intra-sterile, inter-fertile classes would account for such a small percentage of cross-sterility in random crosses, it is obvious that with such a slow-going means of testing the affinities of each individual a clear analysis of a population containing so many groups is impracticable. If the behavior of these self-sterile plants is governed by mendelizing factors, however, then it follows that a series of self-pollinations or of sister-brother matings for several successive genera-

tions will automatically reduce the number of segregating factors and hence the number of intra-sterile, inter-fertile classes. By taking advantage of pseudo-fertility it ought to be possible theoretically to obtain a population of plants belonging to a single class, a population in which every individual is cross-sterile with every other individual, though in this population each individual may fertilize the gametes or be fertilized by the gametes of other populations. These results, predictable on theoretical grounds, were actually obtained. A dozen or so populations with only two intra-sterile classes have been raised and studied, and two populations consisting of a single intra-sterile class have been found. Dr. Anderson has nearly completed an analysis of the precise method by which the controlling factors are inherited. It does not seem advisable for me to discuss these results in detail here as they will be published shortly, but the main facts bearing on the general genetic problem of self-sterility can be stated in a very few words.

First, the behavior of reciprocal crosses is the same. If the pollen of *A* is sterile on *B*, then the pollen of *B* is sterile on *A*. This is an important fact. In many of the populations studied, segregation and recombination of factors for pistil length was such that extremes of 25 mm. and 70 mm. were found. But under the usual conditions for carrying on the work, conditions under which pseudo-fertility was not a disturbing feature, incompatibility of the short-pistiled plant for pollen from the long-pistiled plant was just as marked as when the reverse cross was made. And, similarly, interclass crosses were just as easy to obtain when the long-pistiled plant was the mother as when the short-pistiled plant was used. Dr. Anderson believes that this result is aided by a high positive correlation between the length of "life" of the flower and the length of its pistil. Be that as it may, the growth rate of the pollen tubes in incompatible matings is so slow that even if the flower from a short-pistiled plant remained on the stem for as long a period as with its long-pistiled sister, the tube does not have the opportunity to traverse more than two-thirds of the pistil distance. It is possible, however, so to control conditions that one may sometimes obtain seed from a particular mating when it is impossible to obtain it after a mating made the reverse way. For example, if plant *A*, a plant in vigorous condition and at the height of its flowering season, is used as the pollen parent on an incompatible plant *B*, a plant in weakened condition at the extreme end of its flowering season, some seed will be obtained as a manifestation of pseudo-fertility; but the reciprocal cross is impossible.

A further conclusion may be derived in part from the fact that reciprocal matings are identical when not interfered with by external conditions whose effects are fairly well known and for which reason are controllable and their results predictable. It is to the effect that, though the gametes formed by a particular plant may be packed with many different combinations of genes, as proven by the variable population of zygotes produced, as far as

their activities before fertilization are concerned they behave as if they were all alike. Pollen grains from a single plant may be of variant constitutions with reference to their transmission of qualities to the next generation, therefore, but they show no *selective* fertilization. They are controlled in their gametophytic activities by the genetic constitution of the mother plant on which they are formed. For this reason a genetic experiment conducted in such a manner as to have the critical matings made with pollen from a single plant will give the results to be expected from *chance* matings of germ cells. But one can easily imagine types of genetic matings where the results would be vitiated by not keeping this fact in mind. Suppose, for example, that one desired to make a test mating on plant *A* with pollen from plant *B*. Plant *B* produced little pollen, however, and additional pollen from plant *C* was used because plant *C* was assumed to have the same constitution as plant *B* with regard to the particular factors under investigation. Unfortunately the pollen tubes from the pollen of plant *C* grow faster than the pollen tubes from the pollen of plant *B*, and the resulting zygotes are all sired by plant *C*. Naturally, no geneticist in his right mind would make a test in this way, but nevertheless it may be well to have in mind its possibilities.

Second, the factors which govern the behavior of self-sterile plants are strictly inherited, and are transmitted in accordance with a definite Mendelian mechanism. Class *A*, for example, is class *A* wherever found. A single class has been identified by the cross-sterility test through three successive generations by Dr. Anderson; and the same class has been found in collateral families as far removed as fourth cousins. Thus the behavior of these factors controlling a peculiar physiological difference is exactly the same as that to be found where visually identifiable morphological differences are found.

Third, the genes which govern the behavior of these plants in crosses are numerous. About fifteen classes have been proven to be genetically distinct from each other by proving *each* class to be fertile with *every* other class. Eight or ten other classes have proven to be distinct from all other classes with which crosses have been made; but since every possibility of linking them up with known classes has not been tested, it can not be maintained that they must belong to separate groups. Arguing the matter as a problem in probabilities, however, it can be said that the chances are greatly in favor of there being more than twenty genetically different intra-sterile groups of self-sterile plants in *Nicotiana Forgetiana* and *Nicotiana alata*.

It is greatly to be regretted that it has been impossible to test out thoroughly a good random sample of individuals in these two species. When our work on the self-sterility problem was resumed after the war, only two packets of *N. alata* seed and one packet of *N. Forgetiana* seed would grow. The pedigrees of these seeds were such as to make it highly

probable that each population had been so selected as to reduce the number of intra-sterile groups materially. And so it proved. There were only three or four such classes in each species; and the interesting thing is that no single class of one species was found in the other species or in the classes observed in the descendants of the original hybrids between them which had been made between 1910 and 1912. We can not say therefore whether *N. alata* considered as a species contains any factors governing the behavior of self-sterile plants which are the same as those possessed by *N. Forgetiana*, or not; but from the results obtained we are justified in believing that each species does contain a relatively large number of such factors. They contain such a large number of these factors that the practical result of making random crosses in an unselected population is to obtain such a high percentage of success as to make one believe, with Darwin, that each plant is fertile with the pollen of every other plant.

In conclusion I will say only this: though the study of self-sterility in detail has opened up various fruitful lines of research of which no one can see the end, and though an adequate physiological interpretation of the behavior of incompatible pollen tubes as compared with compatible pollen tubes has not been forthcoming, the genetical problem in its narrow sense, that is to say the problem of the mechanism of its heredity, may be said to be solved. The corroborations of our results coming in from Europe on other species are too exact in detail for one to feel that there is much weight in the criticism that these results refer only to four species of *Nicotiana*. One can only hope that they will be helpful not only to genetic theory, but to the practical problems of the orchardist who has to deal with self-sterile fruits. They do indeed show why whole varieties of asexually propagated fruits are self-sterile. And, further, the work on the causes and control of pseudo-fertility points the way to a practical method of orchard procedure.

BUSSEY INSTITUTION,
HARVARD UNIVERSITY

STERILITY IN RELATION TO HORTICULTURE¹

M. J. DORSEY

The sterility problem in horticulture will be discussed from the standpoint of those factors which limit the crop. Since most of the principles involved are encountered in pomology, the discussion will be limited to this field. Recent investigations have dealt with many of the causes of what the fruit-grower designates as a crop failure. In the broader sense the sterility problem has its setting in the factors which influence the initiation and formation of fruit buds as well as in those which bear upon the set of fruit. It will be evident that, in all of those fruits in which the edible portion includes a ripened ovary, bloom must precede the production of fruit. Let us for the moment, then, keep in mind the point of view of the horticulturist in analyzing the causes which bear upon the set of fruit. Before taking up the discussion of the individual fruits, emphasis will be placed for the sake of clearness upon some general considerations.

First: The variety is the unit in horticulture. Varieties may be discussed in the classroom and in the laboratory in terms of species, but in the orchard and on the market the variety is the unit. The present tendency, however, in breeding horticultural plants to make so many interspecific crosses will tend to bring the characteristics of the species to the foreground, and at the same time, especially in "wide crosses," to increase the difficulties in the setting of fruit because the hybrid condition may have an important bearing upon the formation of pollen and embryo sac.

Second: The ratio between the number of flowers produced and the number of fruit to set, or to mature, varies in the different fruits. In the apple or plum, for instance, a set of five to ten percent of a full bloom is sufficient for a crop. It would be physically impossible for the tree to mature a fruit for each flower in the apple, pear, plum, or peach. On the other hand it is possible for all the pistils in the grape, raspberry, blackberry, strawberry, or currant to set and mature. Likewise, the number of seeds necessary for fruit development varies. Some fruits are seedless, like the banana and the seedless grape; others, like the peach or plum, require a single seed for development; while in the apple and pear the number of seeds present in ripe fruit differs with the variety and also from season to season. In the strawberry or raspberry, where the development of the edible fruit reaches perfection only when a high percentage of the achenes or drupelets set, many more ovules fail to develop in marketable fruit than

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is generally supposed. It will be seen, therefore, that the opportunity for development of both pistil and seed has an important bearing upon the subject at hand.

Lastly, fruit-setting is complicated by the fact that fruit-bud initiation and development accompany fruit-production in some of the fruits, making it necessary to maintain conditions favorable to both. Where fruit buds are formed before dormancy, winter killing, especially in the peach, plum, and cherry, may exceed all other factors in reducing the crop.

When planted alone and pollinated with its own pollen, a variety is self-fertile or self-sterile. Likewise, in mixed plantings the relationship with other varieties is cross-fertile or cross-sterile. The self- or cross-relationship is definite in some combinations and in others is intermediate or variable. With these relationships in mind, let us note briefly the extent of sterility in each of the different fruits as indicated by the more recent investigations.

Status of Sterility in the Different Fruits. In the apple the status of self- and intervarietal-sterility or fertility is not so well defined as in some of the other fruits. The self-sterile, self-fertile, cross-sterile, and cross-fertile conditions occur in all different degrees. Other factors limiting production are alternate bearing, or the so-called "off year," the coming into bearing late of some varieties, as Northern Spy, and the light bearing, even of older trees, which so often happens with Black Twig. The flower of the apple is perfect, and in most varieties the pollen is abundant. Bagging experiments indicate that about two thirds of the varieties are self-sterile (Lewis and Vincent, 1909; Gowen, 1920; Dorsey, 1921). Cross-sterility has been reported in only a few combinations and does not appear to be as important as self-sterility. When there is a full bloom a ten percent set is sufficient for a crop. Cultural conditions have an important bearing upon the formation of fruit buds as well as upon fruitfulness. In the apple, then, self- and cross-sterility, alternate bearing, the light setting of fruit buds, and coming into bearing late are the important considerations. Any one of these, or two or more, acting together may be limiting factors in production.

The pear has many characteristics in common with the apple. The flower is perfect, and normal pollen and pistils are produced in sufficient quantities. A study of 36 of the principal varieties showed that out of this number 22 were self-sterile (Waite, 1895). As in the apple, varying degrees of self- and cross-sterility exist. The size of fruit is correlated with the number of seeds. Cross-pollination is essential to fruitfulness in a number of the most important varieties. Self-sterility was first demonstrated in the pear by Swayne in 1828.

In the peach, sterility has not been found to be an important commercial problem. Investigations at a number of stations indicate that most varieties are self-fertile and cross-fertile, or at least sufficiently so to give an adequate set for a crop (Whitten, 1913; Fletcher 1909-10; and others). On the other hand, in California all varieties of the almond tested were

found to be self-sterile, at least in certain years (Tufts, 1919). Some of the varieties were also cross-sterile.

The varieties of the quince appear to be both self-fertile and cross-fertile.

The plum presents some unusual features in sterility. With but few, if any, exceptions, self-sterility is absolute so far as tests have been made in the varieties of *Prunus americana*, *P. nigra*, *P. besseyi*, and *P. triflora*. In *P. domestica* only about one half of the commercial varieties set fruit when planted alone (Sutton, 1918). Most varieties are cross-fertile, but some cross-sterile combinations have been demonstrated (Dorsey, 1919 b). The flower is perfect and the bloom is profuse. Mixed plantings are necessary to insure a set of fruit with all except those of the European varieties which are self-fertile. As a result of unfavorable weather at bloom, lack of nutrition, and defective pollination, crop failures are frequent.

Judging by the varieties grown at present, sterility seems to be acute in the sweet cherry. All the varieties tested in Oregon were self-sterile (Gardner, 1913), and many of the most important varieties were cross-sterile. Pollen and pistil development appear to be normal. Tests made in other regions show some variation in the degree of self-sterility of the different varieties. Great care must be taken to get the proper varietal relationship in the orchard to avoid light crops from this source.

In the grape the named varieties can be thrown into two distinct groups, one of which is self-fertile and the other self-sterile. The self-sterile and also the cross-sterile condition are associated with the reflexed stamens and defective pollen. The flower type furnishes a reliable guide for mixing varieties in planting to insure pollination. The importance of self-sterility in the grape and the care which must consequently be taken in planting are shown by the fact that out of 132 of the more important commercial varieties 37 have reflexed stamens.

The unfruitfulness of many varieties of the strawberry when planted alone is widely known. Here, as in the grape, self-sterility is correlated with flower type. Where normal pollen is produced there appears to be no incompatibility in either the self- or the cross-relationship (Valleau, 1918). On account of the unfruitfulness of the pistillate varieties, breeders have favored the staminate types; out of 62 of the varieties most extensively grown, only 10 are classified as pistillate (Fletcher, 1917). The dioecious condition in the strawberry also influences the functional activity of anther and pistil. Fertility, either self- or cross-, decreases in the later flowers of an inflorescence to such an extent that only the primary or secondary flowers form fruit. This condition has been best illustrated in unnamed seedlings at the Minnesota station which were of course discarded. Most varieties produce pollen in abundance, and aborted pollen is found to the greatest extent in the staminodia.

Tests made with the brambles show that self-sterility exists to a much greater extent than has been suspected. Even in carefully controlled

crosses the number of achenes which develop is surprisingly limited. In North Carolina, 11 out of 15 varieties of dewberries and 4 out of 16 of the blackberries were found to be self-sterile (Detjen, 1916). In mixed plantings Ancient Britain sometimes sets lightly. In the brambles a considerable number of drupelets can fail to develop before the berries become unmarketable. Counts made with ripe red raspberries (varieties Cuthbert and Latham) showed that as many as ten to fifteen percent of the drupelets had failed to develop in apparently perfect berries; when the percentage ran higher than this, both size and uniformity were affected.

In the currant and the gooseberry, self- and cross-sterility results in the loss of flowers from the clusters, especially at the tip, and in small fruits with few seeds. Imperfect clusters vary with the season and variety, but pollination and position appear to be important factors. In the black currant the pollen is sticky, and artificial pollinations resulted in nearly a perfect set in some varieties (Wellington, Hatton, and Amos, 1921; Hatton and Amos, 1921). In these varieties the length of the style proved to be an important consideration, because self-pollinations took place when the style was long enough to bring the anthers in direct contact with the stigma. Of the black currants studied, all varieties were self- and cross-fertile. The dropping of flowers, generally from the terminal part of the cluster, is one of the most serious difficulties in the currant.

This phase of the subject might be discussed further, but the above summaries will suffice to illustrate the status of fruit-setting in the principal fruits. It will be seen that the sterility problem is different in each and that it varies in degree of importance. A critical survey of the general condition reported above indicates that the factors which condition fruit-setting may be thrown roughly into three main categories, namely, weather, genetics, and nutrition. These will be considered more in detail in the order of mention.

The treatment of these will be clearer if a classification is made at this point of the possible fate of flowers. A study of the life history shows three distinct periods of dehiscence. These are: (a) the first drop, which includes all pistils in which growth is stopped before the embryo sac is completely formed; (b) the second drop, which includes all pistils in which fertilization has failed to take place; and (c) the third, or June, drop, which is made up of those fruits in which the embryo has aborted. This classification does not take into account winter killing or spring frost injury. The effect of the loss of pistils at the different drops will vary with the fruiting habit. It will be seen, then, that there are certain definite causes to which the loss of flowers which do not mature must be attributed.

The Relation of Weather to the Set of Fruit. Unfavorable weather causes more crop failures and irregularities in production than any other single cause. Fruit buds may be injured by low temperatures during dormancy or after growth has started following the break in the rest period, in late

winter or early spring. Freezes and frosts are destructive to flowers and young fruits, but periods of low temperature during bloom may be just as damaging to the crop. Storms of short duration do not necessarily interfere seriously with the set. Strong winds, rains, cloudy weather, and low-temperature periods influence pollen dissemination directly, and indirectly through hindrances to insect activity.

In addition to the factors mentioned above, weather may have a detrimental influence upon the processes taking place at bloom, especially by delaying them. The length of time that pollen is available after dehiscence varies from a few hours to a day or so according to the weather and to the succession in the opening of the anthers. In most seasons there appears to be sufficient dissemination of pollen if it is available.

Stigmas remain receptive under orchard conditions from two to six days. This time may also be considered as the length of life of the stigma. Delays in pollination subtract just so much from the time left before the abscission of the style or disintegration in the egg, which in the apple begins as early as 120 hours after bloom (Knight, 1917), while in the plum the egg appears normal two weeks after the bloom and can still be recognized 33 days afterward (Dorsey, 1919 *b*). The rate of pollen-tube growth becomes of vital importance in relation to fruit-setting when pollination is delayed, when the length of life of the egg is short, or when the growth rate of the pollen tube is retarded by low temperatures during bloom.

On account of the time limit set by the period of activity of the processes taking place at bloom, adverse weather affects fertilization chiefly by causing delay. This appears to be more of a hindrance than direct injury from rain or wind. Aside from killing by frosts and freezes, the effect of weather is indicated at the second or the non-fertilized drop by the loss of flowers in the apple, plum, peach, or cherry, by imperfect clusters in the grape or currant, and by imperfect fruits in the strawberry and raspberry.

Genetic Considerations. The genetic factors inherent in horticultural material which affect the self- and cross-relationship are encountered in dioeciousness, in self- and cross-sterility, and in aborted sex structures. It was shown in the discussion on the status of sterility in the different fruits that these considerations present a serious problem to the grower in a large number of the most important varieties.

The dioecious condition is encountered in the grape and the strawberry. Since incompatibility is practically absent in both, the flower type may be taken as a guide to both the self and intervarietal relationship. Intermediate stages in stamen development which produce defective pollen and apparently normal pistils which, however, do not function (Valleau, 1918) have been confusing to growers. Likewise, in the grape the pollen borne by the reflexed stamens of the pistillate varieties, while forming no germ pore but having a defective generative nucleus (Dorsey, 1914), yet has much the same external appearance as other grape pollen. The failure to recognize

the unfruitfulness of the pistillate varieties has been expensive in many instances, and this mistake is still frequently made in new plantings.

Self- and cross-sterility as found in the apple, cherry, plum, and other fruits is the type resulting from slow pollen-tube growth. It has not been demonstrated as yet whether the gametes would unite if brought together. Incompatibility does not appear to be influenced greatly by nutrition. In such extreme cases as the native plums, self-sterility has not been changed to self-fertility under the conditions of any of the tests, and in controlled crosses self- and cross-sterility are encountered on the same tree with cross-fertile combinations. Pollen germination takes place in both the self-sterile and cross-sterile relationship, although tube growth is slow and variable in length from different grains. The effect of incompatibility on the crop appears at the second drop and may be as detrimental as that of dioeciousness.

Pollen abortion is extensive in the hybrid varieties. Aborted grains become turgid in contact with a receptive stigma but do not send out tubes. Pistil abortion, however, does not appear to be so extensive. In some of the hybrid plums, all the pistils develop normally while more than half of the pollen may be aborted. If the chromosome combinations condition development in the pollen, why not also to the same extent in the egg? The probable explanation for this difference lies in the tetrad of megaspore nuclei where a replacement could take place if any one of the four cells could form the embryo sac in case the others were aborted. This adjustment would theoretically allow for only one fourth as much abortion in the embryo sac as in the pollen grain. It is interesting to note in this connection that deficient nutrition causes more extensive pistil abortion in the plum than pollen abortion. Pollen abortion has but little influence upon fruit-setting, except in those few cases where it is complete, because of the quantity of normal pollen produced by most fruits.

Embryo development may also be conditioned by genetic factors. The June or third drop is composed for the most part of young fruits in which the embryo ceases growth, and consequently is a measure, at least in some instances, of genetic influences although it is also greatly affected by nutrition. To illustrate, in the cross Compass \times Yellow Egg 652 flowers out of 1,327 set, but only 8 matured, as contrasted with the cross Compass \times Burbank in which 116 fruits set out of 175, and 114 matured. The influence of embryo abortion is much more sharply defined in the fruits with one seed than in those with more than one, and this phase of the varietal relationship must be considered along with many others in finally deciding upon pollenizers.

It will be seen, then, that fruit-setting is influenced by genetic considerations which are independent of the influence of weather or of nutrition. These may affect the first drop through abortion in the embryo sac, the second drop through slow pollen-tube growth as a result of incompatibility,

and the third through embryo abortion. As to just how far genetic factors enter in the failure of so many normal-appearing pollen grains to germinate or of apparently normal seeds to grow, it is difficult to state because so many other considerations also enter.

Nutritional Considerations. The research on the relation between nutrition and sterility, or the broader question of fruit-setting, while not easy to summarize, points to a solution of many phases of the problem. The results include and overlap some things which have heretofore been given other interpretations, and have progressed from a study of the effect of nutrition on the plant as a whole to a study of the effect on the fruiting unit, such as the branch, spur, node, or even the individual flower. Nutritional studies are complicated by the variations encountered in seasons, soils, moisture supply, and in the nutritional requirements of the several horticultural crops.

Some things, however, appear to be well established. The importance of size of plant or tree in relation to yield is becoming recognized, especially in the tree fruits. The primary factors in obtaining size appear to be nitrogen and soil moisture. The whole orchard program should be directed toward a control of these two factors as they bear upon the extension of the fruiting area, fruit-bud initiation and formation, fruit-setting, fruit maturity, dormancy, and hardiness. The early period of rapid growth, of the tree fruits particularly, should be kept in mind, because fruit-bud initiation and formation accompany the period of vegetative extension. While many of the details have not as yet been worked out, it appears that the most favorable conditions for growth, fruit-bud initiation and development, and fruit-setting and maturity may be somewhat conflicting. The conception of the carbohydrate-nitrogen balance (Kraus and Kraybill, 1918) furnishes a workable basis for cultural practices, and the control of fruitfulness depends primarily upon proper pruning, the application of nitrogen, and the conservation of moisture.

While skilled growers have for some time recognized the unfruitfulness of exceptionally vigorous as well as of exceptionally slow-growing plants, the variation in the response of the different fruits complicates the control of fruitfulness. For instance, in the apple young trees, or old trees heavily pruned, are generally found to be unfruitful, and some varieties may be fruitful when interplanted with others which are unfruitful. In fact, York Imperial is sometimes so near the border line between the fruitful and non-fruitful conditions that some limbs on a tree bear fruit while others on the same tree do not. In the peach, on the other hand, yield is closely correlated with vigor (Alderman, 1915). Likewise, the red raspberry responds very readily to nitrogen (Chandler, 1920) and is seldom oversupplied with it, while the black raspberry and blackberry make less response. In general, however, these differences are limited, and up to a certain point in all species, size of fruit and yield accompany strong growth.

One phase of sterility quite disappointing to growers, and due primarily to deficient nutrition, is the production of a heavy bloom from which no fruit is set. This is encountered in the apple, in the plum, and probably to a lesser extent in other fruits, and may include a part of the flowers or all of them. While the effect of deficient nutrition may be different in the several fruits, in the plum the method of expression is pistil abortion (Dorsey, 1919 *b*). The same is also probably true in the apple. In the strawberry and the raspberry, deficient nutrition may result in imperfect berries on account of the poor set of achenes or drupelets. A different condition is encountered in the currant, in some of whose varieties there is as much as ten days to two weeks between the time of opening of the basal and of the terminal flowers. In such instances, the currants at the base enlarge considerably before the terminal flowers open, with the result that the latter drop leaving the bare stem of the cluster. The status of individual flowers in the currant has much in common with the more extreme condition encountered in the apple or plum. In all the fruits which produce an excess of bloom, the position of the individual flower appears to have much to do with its opportunity for development. In the plum, for instance, the flowers borne on the terminal growth come into competition with fruiting laterals, formed soon after bloom at each node, with the result that flowers borne in this position seldom set. Some tests were made at the Minnesota station with the currant to determine the relation between the position of the flower and setting. When the basal flowers were removed from selected clusters before they opened, the terminal ones set, although they had fewer seeds and were smaller. On the same bush under the same field conditions, terminal flowers on clusters not so treated dropped.

With the carbohydrate-nitrogen conception as a background, the trend of the more recent investigations may be illustrated by the work with the apple. Some varieties are known to growers as annual, and others as "off-year" or biennial bearers. For a long time thinning has been advocated as a means of preventing exhaustion and consequently inducing annual bearing. In New York, four years' thinning did not make Baldwin more regular in bearing (Gourley, 1915). Similar results were obtained in West Virginia with Grimes and Delicious (Auchter, 1919). Spurs which fruit one year seldom bloom the next (Auchter, 1919; Roberts, 1920), and recent investigations indicate that, if thinning is to influence fruit-bud formation on spurs which have bloomed, the removal of buds or flowers at least before they set (Roberts, 1920) rather than of the fruit, is required (Crow and Edit, 1921). The suggestions which have come from the later studies as to methods of correcting the "off-year" include good cultural methods (Gourley, 1915), pruning out crowding branches and cutting back to rejuvenate the spurs (Roberts, 1920), stimulation of alternating spur blooming by pruning and fertilization (Roberts, 1920; Crow and Edit, 1921), and obtaining the normal fruit-spur formation on the two-year-old wood

(Roberts, 1920). While tree performance during the bearing and "off-years" indicates marked variability in the physiology of the tree as a whole, spur analyses and defoliation experiments show a similar difference more locally (Heinicke, 1917; Wiggans, 1918; Hooker, 1921, and others).

Control Measures. It may be of interest to investigators in other fields to note briefly some of the methods of controlling sterility which have been worked out to date. The remedy is of course suggested largely by the cause. Means of counteracting the influence of unfavorable weather have been given less attention than nutritional genetic causes. Orchard heating has been used more in the West than in the East and is effective only within a limited range. There may be some advantage in some seasons in extending the period of bloom either by a succession of varieties or by an extended period of bloom with the variety, but this is not always effective in avoiding the effects of prolonged adverse weather. There may be some promise of control within narrow limits from the use of pollenizers whose pollen will develop tubes at lower temperatures than others. This suggestion comes from some of the hardier plums from northern sources. There is a still more readily available remedy in the early application of nitrate of soda, which has given some indication of effectiveness in recent preliminary tests. All told, however, weather will still prevent the set in spite of any of the remedies yet tried when extreme conditions are encountered.

Given favorable weather and growth conditions, a remedy for the genetic causes of sterility is found in mixed planting. This phase of sterility has been given considerable attention, and control measures are well known as a result of the studies made of the self- and cross-relationship of varieties. The effect of aborted pollen, the dioecious condition in the grape and the strawberry, as well as incompatibility, are all counteracted by properly mixing varieties. In fact, the problem can be eliminated in the grape and strawberry by the selection of varieties with perfect flowers. Two methods have come into common use in mixing varieties for pollination purposes—top working and inter-planting. The former is usually adopted in older plantings to correct mistakes and the latter in new plantings. Serious errors have been made in some orchards by planting trees or vines alternately in the rows instead of in narrow blocks or strips. When varieties are planted alternately in this way, both spraying and harvesting are made more difficult. In making mixed plantings careful attention should be given to the relative time of dehiscence of the anthers and to the receptiveness of the stigma.

The details of bringing about the optimum nutritional conditions for fruit-bud initiation and formation, fruit-setting, and fruit-development have as yet only been approached. The control of the carbohydrate-nitrogen-moisture ratio appears to be a workable point of attack. The investigations to date are sufficiently definite to indicate that each of the fruits presents a problem different in many respects. On account of the

bearing on the whole orchard program this field needs further intensive investigation.

An attempt has been made in the preceding discussion to survey the general question of fruit-setting and to evaluate the different factors which have a bearing upon it. It will be seen that these can be assigned to three general causes each of which although influenced by the other may become the dominant consideration. The total effect of these in reducing the crop can best be appreciated by those familiar with reduced yields and crop failures. The investigations in some phases of the problem have gone no farther than to emphasize the need of further work. The fact that fruit for the most part is produced under such variable conditions will of necessity make the set uncertain. There are certain factors, however, some favorable to fruit-setting and some unfavorable, which may be regarded as fixed or constant in their relation to fruit-setting. While the investigations in this field have gone far toward devising means of stabilizing the industry, much more remains to be done.

WEST VIRGINIA UNIVERSITY,
MORGANTOWN, W. VA.

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GENERA OF NORTH AMERICAN FABACEAE
I. TRIBE GALEGEAE

P. A. RYDBERG

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The tribe Galegeae has been divided since Bentham's time into seven subtribes. Of these one has already been raised to tribal rank, Psoralieae, which is characterized by the glandular-punctate foliage and by the pods, which are one- or few-seeded, usually indehiscent but rarely breaking open irregularly across the middle, never valvate. Another subtribe should be removed as a tribe Indigofereae, having three characters seldom found elsewhere in Fabaceae and never combined in any of the tribes. These are malpighiaceae hairs (appressed hairs, 2-branched with branches forming a straight line, the hairs therefore apparently attached at their middle), appendaged connectives in the anthers, and lateral spurs on the keel-petals. It may be that Glycyrrhiza and one or two genera should be removed also and form another tribe, on account of the indehiscent (though several-seeded) glandular fruit and confluent anther cells.

After the removal of the two subtribes mentioned, the tribe may be characterized as follows:

Herbs, shrubs, or trees, or woody vines, without glandular dotted foliage (except in Glycyrrhiza). The leaves are odd-pinnate or abruptly pinnate, with or without stipels, very rarely with malpighiaceae hairs. The calyx is campanulate to tubular, 5-toothed or 5-lobed, rarely more or less 2-tipped. The corolla is papilionaceous, with 5 petals, the two keel-petals more or less adnate along the lower margins. The stamens are 10, diadelphous or monadelphous, the connective without appendages. The ovary is usually many-ovuled, more or less curved or bent upwards; the style slender and the stigma small. The fruit is several- or many-seeded, 2-valved, usually dehiscent.

As stated before, Bentham and Hooker acknowledged 7 subtribes. These authors were closely followed by Taubert in Engler and Prantl's *Natürlichen Pflanzenfamilien*. Taubert's key in translation reads as follows, after the Indigofereae and Psoralieae have been removed:

- α. Seeds strophiolate. Flowers in 2's in the leaf-axils or forming a terminal raceme (compare Tephrosia and Fordia). c. BRONGNIARTIINAE.
- β. Seeds not strophiolate.
 - 1. Inflorescence racemose, terminal, opposite the leaves, or on the branches paniculate, more rarely in the axils of the upper leaves or all peduncles or only the lower paired or clustered in the axils. Stipe inside the staminal sheath sometimes surrounded by a small cup-like disk. d. TEPHROSIIINAE.

II. Inflorescence always axillary. Stipe without disk at the base.

Pod flat, when inflated at least the endocarp flat, 2-valved. *e. ROBINIINAE.*

Pod inflated or bladdery, rarely flat, then 2-celled lengthwise.

Style bearded above; pod inflated or bladdery, not dehiscent or opening only at the apex, more rarely 2-valved, never with a longitudinal partition. *f. COLUTEINAE.*

Style naked, more rarely hairy like a brush around the stigma; pod 2-celled or nearly 2-celled lengthwise, seldom 1-celled. *g. ASTRAGALINAE.*

From this key it is evident that the subtribes are very artificial and that it has been very hard to find really good distinctive characters. It is also evident that these characters have been drawn without taking into consideration the American genera in full, in which they break down repeatedly.

While the strophiole is very well developed in the Brongniartiinae, in fact better so than in any other group in the Fabaceae, strophioles are present, although small, in several species of Cracca.

The Tephrosieae of Benthham (Tephrosiinae of Taubert) is in itself not a natural division, for Barbiera is not at all closely related to the rest, being distinguished by the long-clawed petals, the presence of 2 bractlets beneath the tubular calyx, and the style bearded along the upper side. In fact, it has no close relative in the whole tribe. The paired bractlets are found in Sesban and related genera and in Diphysa, which are all included in the Robinieae of Benthham (Robiniinae of Taubert).

Neither does Krauhnia seem to be closely related to Cracca or Galega, but apparently forms a natural group with several Asiatic genera, especially Millettia.

The position of the inflorescence, being either terminal or apparently opposite the leaves, a character very important in the minds of both Benthham and Taubert, seems to be of little value, for in many species of Galega and a few of Cracca (see explanation under Cracca) the inflorescence is axillary, just as in the Coluteinae and Astragalinae. The other character, the presence of the disk at the base of the staminal sheath, is also unreliable, for, while it is fairly well developed in Cracca and Krauhnia and their relatives, it is not at all in Barbiera.

The Robinieae of Benthham (Robiniinae of Taubert) is distinguished from the Coluteae and Astragaleae (Coluteinae and Astragalinae of Taubert) by the one-celled, two-valved, flattened, not inflated pod, but in the genus Diphysa, included in the first, the exocarp is strongly inflated, forming two lateral elongate bladders, and in Homalobus and Kentrophyta, segregates of Astragalus, the pod is decidedly compressed and fulfills all the characters ascribed to the Robinieae. In Benthham and Hooker's *Genera Plantarum* the following remarks are made: "In Astragalus paucis [legumen] planissimum est, sed membranaceum et perfecte septatum." This statement applies to *Hamosa* Med., a segregate of *Astragalus* found both in the Old

World and America, in which the pod is flat and 2-celled. In *Atelephragma* Rydb., another segregate found only in America, the septum is incomplete, while in *Homalobus* and *Kentrophyta*, both exclusively American, there is not a vestige of a partition and the fruit is exactly like the fruit of *Poiteoa*, *Coursetia*, or *Corynella*, placed in the *Robinieae*.

Both Bentham and Hooker, and Taubert seem to have ignored or else knew imperfectly these segregates of *Astragalus* when characterizing their subtribes. In *Benthamantha*, also placed in the latter subtribe, the pod is also similar but with false transversal partitions. In *Sesban* and *Daubentonia*, both referred to *Robinieae*, the pod is hardly compressed, in the former terete or nearly so, in the latter 4-angled. There is therefore no definite line between these three subtribes as constituted by Bentham and Hooker and by Taubert, nor are the *Brongniartiae* or the *Tephrosieae* very distinct.

The classification must therefore be remodeled along other lines. I shall give here a tentative reclassification, which will probably be modified when more study has been made on the *Astragalinae*.

Seeds strophilate; embryo with a straight radicle;
flowers 1 or 2 in the axils of the leaves or in terminal
racemes or panicles; calyx subtended by a pair of
deciduous bractlets; pods flat; trees or shrubs.

Subtribe 3. *BRONGNIARTIANAE*.

Seeds not strophilate (rarely slightly so in species of
Cracca); embryo mostly with an incurved radicle;
flowers mostly racemose.

Bractlets 2 under the calyx; pods internally with
more or less distinct false cross-partitions.

Calyx tubular, with long lobes; petals long-
clawed, their blades cuneate at the base, that
of the banner oblong, not spreading; pods flat,
many-seeded, dehiscent; shrubs with odd-
pinnate leaves.

Subtribe 4. *BARBIERIANAE*.

Calyx campanulate, with short tooth-like lobes;
petals short-clawed, at least the blades of
the wings with basal auricles; blade of the
banner sub-orbicular or broadly ovate;
pods not flattened or if flat 2-seeded
(*Glottidium*).

Exocarp of the pod not inflated; hypanthium
obsolete, not differentiated from the calyx;
shrubs or trees, with abruptly pinnate
leaves.

Subtribe 5. *SESBANIANAE*.

Exocarp of the pod inflated, forming two
elongate bladders, one on each side of the
pod; hypanthium well developed and dif-
ferentiated from the calyx, obconic; shrubs
and trees, with odd-pinnate leaves.

Subtribe 6. *DIPHYSANAE*.

Bractlets under the calyx wanting; pods usually
without cross-partitions, except in *Bentha-*
mantha, *Sphinctospermum*, and *Hebestigma*.

Base of the pistil or of its stipe usually surrounded by a more or less developed saucer-shaped disk within the staminal sheath; racemes terminal, or terminal and in the upper axils, or opposite the leaves, or if axillary, the leaflets with parallel oblique lateral veins.

Leaflets with parallel or indistinct lateral veins; pods obliquely striate; leaves without stipels; herbs or low shrubs.

Subtribe 1. CRACCANAE.

Leaflets netted-veined; pods not obliquely striate; leaves mostly with stipels; trees or (ours) woody vines.

Subtribe 2. MILLETTIANAE.

Base of the pistil or its stipe not surrounded by a disk; racemes always axillary; leaflets not with parallel oblique lateral veins.

Pods flat, or if terete with prominent sutures, neither inflated nor with even a vestige of a longitudinal partition.

Flowers in fascicles, on short branches arising in the axils of fallen leaves; leaves abruptly pinnate; banner usually enveloping the other petals.

Subtribe 7. CORYNELLANAE.

Flowers in axillary racemes; leaves odd-pinnate, except in some species of *Coursetia* and occasionally in *Olneya*; banner mostly spreading.

Subtribe 8. ROBINIANAE.

Pods more or less inflated or completely or partially 2-celled, by the intrusion of one or both sutures.

Style bearded along the upper margin; pods always 1-celled and inflated.

Subtribe 9. COLUTEANAE.

Style glabrous, or bearded only around the stigma.

Anther-cells not confluent; pods not prickly; plant not glandular-dotted.

Subtribe 10. ASTRAGALANAE.

Anther-cells confluent at the apex; pods in ours prickly; plant glandular-dotted.

Subtribe 11. GLYCYRRHIZANAE.

SUBTRIBE I. CRACCANAE

Herbs or shrubs, with alternate odd-pinnate leaves, persistent stipules, but no stipels, the leaflets usually with parallel oblique lateral veins. The flowers are racemose. The calyx is campanulate 5-lobed, but the upper lobes are often more or less united. The corolla is truly papilionaceous, the petals are more or less clawed, the banner is broad and spreading. The stamens are monadelphous or diadelphous, inserted on a more or less developed campanulate disk. The style is glabrous throughout or more or less hairy around the stigma. The legume is elongate, flat, 2-valved, usually obliquely striate. The seeds are reniform or transversely oblong, *i.e.*, their longer axis parallel to the axis of the pod.

The subtribe contains, besides the following three genera, a few confined to the Old World. *Cracca* is cosmopolitan of warmer regions, *Peteria* is endemic American, and *Galega* is Eurasian, introduced in the New World. Stipules not spinescent; lateral veins of the leaflets prominent.

Upper filaments wholly united with the staminal sheath, forming a closed

tube; banner in ours glabrous.

1. *GALEGA*.

Upper filament free, at least at the base; banner strigose on the back.

2. *CRACCA*.

Stipules spinescent; upper filament free; lateral veins of the leaflets obsolete.

3. *PETERIA*.

1. *Galega* [Tourn.] L. Sp. Pl. 714. 1753

Perennial herbs. The leaves are odd-pinnate, with semi-sagittate stipules. The flowers are in axillary or terminal racemes with narrow bracts and no bracteoles. The calyx has 5 subequal lobes. The corolla is white or light blue; the banner is obovate-oblong, narrowed below into a very short claw; the wings have an oblong blade with a prominent basal auricle, and a longer claw, and are adherent to the keel at the middle; the keel-petals are obtuse, more or less arcuate, longer than the wings, and united nearly their whole length. The filaments are monodelphous, *i.e.*, all united into a sheath. The ovary is sessile, many-ovuled; the style glabrous; the stigma small, terminal. The pod is linear, terete, 2-valved, sometimes constricted between the seeds. Seeds are transversely oblong, without strophiole.

ILLUSTRATION: Plate XXXIII A. *Galega officinalis* L., $\times 2/3$; 1. calyx, 2. banner, 3. wing, 4. keel-petal, 5. staminal sheath, 6. pistil, $\times 2$; 7. pod, $\times 1$; 8. cross section of pod, 9. seed, $\times 2$.

In the *Species Plantarum*, the genus *Galega* contained only one species, *Galega officinalis* L., which therefore is the type.

Synonyms:

Calotropis G. Don. Gen. Syst. 2: 228. 1832. Type: *C. tricolor* (Hook.) G. Don., based on *Galega tricolor* Hook., which is supposed to be the same as *G. officinalis* L.

Accorombona Endl. Gen. 1427. 1841. This was a substitute for *Calotropis* G. Don., not *Calotropis* R. Br. 1809. Hence the same type.

The genus consists of 4 or 5 species native of southern Europe and the Orient. Of these, *G. officinalis* is sometimes cultivated as a forage plant and in olden times was used in medicine. It has been found occasionally in the western states from Kansas to Utah, as an escape from cultivation or introduced incidentally among seeds. The genus is closely related to *Cracca*, differing mainly in the monadelphous stamens. The racemes are mostly axillary, and therefore the genus is, according to Bentham and Hooker, anomalous in their subtribe *Tephrosieae*, but, as will be shown, this abnormality is found even in species of *Cracca*.

2. *Cracca* L. Sp. Pl. 752. 1753

Herbs, often woody below, or shrubs. The leaves are odd-pinnate, the leaflets striate, with veins oblique to the midrib and parallel; the stipules

are setaceous, or broader and striate. The flowers are racemose, the racemes are either terminal, with or without smaller racemes in the upper axils, or apparently opposite the leaves, or rarely axillary. The individual flowers are usually in clusters of 2-6 at each node of the peduncle. The calyx is campanulate, furnished with a more or less developed disk; the lobes are five, either subequal or the lowest one longer, the upper two usually more or less united. The petals are clawed; the blade of the banner is sub-orbicular, more or less sericeous without; the blades of the wings are oblong or obliquely obovate, slightly coherent with the keel, with a more or less developed basal auricle; the keel-petals are more strongly lunate with a larger basal auricle. The stamens are usually partly monadelphous, the uppermost filament at first free from the staminal sheath at the base, adnate to it at the middle, and often separating from it later. The ovary is sessile, many-ovuled, the styles inflexed or incurved, somewhat horny at the base, most commonly glabrous, the stigma terminal. The pod is sessile, flat, 2-valved, many-seeded.

ILLUSTRATION: Plate XXXIII B. *Cracca virginiana* L., $\times 2/3$; 1. calyx, 2. staminal sheath, 3. pistil, 4. banner, 5. wing, 6. keel-petal, 7. pod, $\times 1$; 8. pod in cross-section, 9. seed, $\times 2$.

The genus was first established in Linnaeus' *Flora Zeylanica* 1747. The first species described both in this book and in *Species Plantarum* is *C. villosa*, which must be regarded as the type.

Synonyms:

Brissonia Neck. Elem. 3: 36. 1790. No type was given, but the genus was based on "some species of *Galega* L." [Necker's reference indicated the 14th edition of Linnaeus' *Systema Vegetabilium*.] The first botanist to assign species in the genus was Desvaux (*Jour. Bot.* 3: 78. 1814), who proposed *B. trapesicarpa*, *B. stipularis*, and *B. coronillaefolia*, but none of these are found in Linnaeus' work named above. De Candolle (*Prod.* 2: 249. 1825) adopted *Brissonia* as a section under *Tephrosia*. Of this section apparently *T. toxicaria* Pers. should be regarded as the type.

Reineria Moench, Meth. Suppl. 44. 1802. Type: *R. reflexa*.

Tephrosia Pers. Syn. Pl. 2: 328. 1807. It was based on 39 species, without definite type. The first species is *T. filifolia*, but the type ought to be sought in the second and larger division with pinnate leaves.

Kiesera Reinw. Syll. Pl. Nov. 2: 11. 1828. Type: *K. sericea* Reinw., which is supposed to be the same as *Tephrosia candida* DC.

Apodynomene E. Meyer, Conn. Pl. Afr. Aust. 111. 1835. Type: *E. grandiflora* (Pers.) E. Meyer, based on *Tephrosia grandiflora* Pers. This is the first and best known species.

Catacline Edgew. Jour. As. Soc. Beng. 16: 1214. 1847. Type: *C. sericea* Edgew.

Macronyx Dalz. Hook. Kew Jour. 2: 35. 1850. Type: *M. strigosus*, which is close to if not identical with *Tephrosia tenuis* Wall. Perhaps this should be excluded from the synonyms of *Cracca*.

Balboa Liebm. Vidensk. Meddel. 1853: 106. 1854. Type: *Balboa diversifolia* Liebm., the only species.

Seemannantha Alef. Bonplandia 10: 264. 1862. This was a substitute for *Macronyx*, and hence based on the same type.

Cracca is a large genus, probably containing about 150 species, found in warmer regions of both hemispheres. In North America (including Central America and the West Indies), there are 72 species, of which 65 are native and 7 introduced.

Taubert divided the genus into 4 sections: *Brissonia*, *Reineria*, *Pogonostigma*, and *Requienia*. Of these the last two, which are not represented in America, should be removed as distinct genera, having 1-seeded fruits.

The principal character by which Taubert distinguished the first two sections was the relative width and length of the calyx lobes. Some species, as for instance *C. leucantha*, which has long and narrow calyx-lobes, really belong to *Brissonia* instead of *Reineria*. A better distinction is the inflorescence, which is monopodial in the former and sympodial in the latter. In the monopodial inflorescence the terminal raceme is best developed, but many of the species bear also secondary racemes in the upper axils. In the sympodial inflorescence the terminal raceme develops first, but in the uppermost leaf-axils a branch is produced which in its turn develops a terminal raceme; this is repeated several times, and the racemes therefore appear to be opposite the leaves. In a few species, as for instance *C. rhodantha*, *C. foliosa*, *C. vicioides*, and *C. Brandegei*, the racemes are mostly at the nodes, but neither opposite the leaves nor strictly axillary; they are inserted in the axils but obliquely, *i.e.*, not in the plane determined by the stem and the rachis of the leaves. The monopodial or sympodial character is not perfectly clear.

Several of the species are used as a fish-poison by the natives of the region where they grow, others for poisoning arrows in Southern Africa; still others furnish a blue dye, somewhat resembling indigo.

3. *Peteria* A. Gray. Pl. Wright 1: 50. 1852

Perennial herbs, somewhat woody at the base. The leaves are odd-pinnate with spiny stipules. The flowers are usually in terminal racemes. The calyx is cylindro-campanulate, gibbous at the base above; 5-lobed with the upper two lobes united high up. The corolla is ochroleucous or nearly white, the banner long-clawed with an oblong-obovate blade; the wings have an obliquely oblong blade, slightly auricled at the base, and a slender claw; the blades of the keel-petals are obliquely obovate, obtuse, with a broad, rounded basal auricle. The stamens are diadelphous, with the upper filament wholly free. The ovary is short-stipitate or sessile, many-ovuled, the style with a horny base, inflexed, glabrous, except at the apex, where there is a ring of hairs. The pod is linear, straight, compressed, 2-valved, many-seeded, with thick sutures.

The genus was based on a single species, *P. scoparia* A. Gray, and con-

sists of three species of southwestern United States and northern and central Mexico. In habit the species resemble some species of *Astragalus* and its segregates, but the racemes are not axillary but terminal, or when an axillary branch is developed become apparently opposite the leaves as in *Cracca*. The spinescent stipules constitute also a distinctive character. The genus is evidently related to *Cracca*, but the hair-tufts around the stigma and the less distinct veining of the leaflets obscure the relationship.

ILLUSTRATION: Plate XXXIII C. *Peteria scoparia* A. Gray, $\times 2/3$; 1. calyx, $\times 2$; 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, $\times 1$; 7. pod of *P. glandulosa*, $\times 2/3$; 8. cross section of the same, $\times 2$; 9. seed, $\times 2$.

SUBTRIBE 2. MILLETTIANAE

Trees or woody vines with alternate odd-pinnate leaves and persistent stipules, usually also with stipels. The calyx is campanulate, 5-toothed, but the lobes are often minute, or the upper 2 and the lower 3 more or less united, forming an upper and a lower lip. The corolla has short-clawed petals, the banner being broad, spreading or reflexed. The stamens are monadelphous or diadelphous, the upper filament free at least at the base. The pod is flat, 2-valved, elongate, several-seeded. Seeds mostly reniform.

Besides the following genus which is represented by native species in the eastern United States and eastern Asia, the subtribe consists of four or five Asiatic and perhaps two African genera.

4. *Kraunhia* Raf. Med. Rep. N. Y. II, 5: 352. 1808

High-climbing woody vines with odd-pinnate leaves, small stipules and stipels. The flowers are in terminal racemes, with deciduous bracts. The calyx is more or less 2-lipped, the upper lip with 2 broad teeth united to near the apex, the lower with 3 longer teeth. The corolla is blue or purple, rarely white, the petals are subequal in length; the banner has a suborbicular blade, reflexed, and with 2 callosities or appendages, the claw is short; the blades of the wings are obliquely obovate, falcate with a large basal auricle on the upper edge and often a smaller one on the lower; the keel-petals are clawed, united at the apex, the blade is lunate with a sharp basal auricle. The stamens are diadelphous, the upper stamen is free or slightly adherent at the middle. The ovary is stipitate, many-ovuled, glabrous; the style inflexed, glabrous; the stigma small. The pod is elongate, flat, 2-valved. The seeds are reniform, without strophiole.

ILLUSTRATION: Plate XXXIII D. *Kraunhia frutescens* (L.) Greene, $\times 2/3$; 1. calyx, 2. stamens, 3. pistil, 4. banner, 5. wings, 6. keel-petals, $\times 1$; 7. fruit, 8. the same in cross section, $\times 2/3$.

The genus was established on *Glycine frutescens* L. without a diagnosis. Synonyms:

Diplonyx Raf. Fl. Ludov. 101. 1817. Type: *D. elegans* Raf., which is regarded as the same as *Kraunhia frutescens* (L.) Greene.

Thysanthus Ell. Jour. Acad. Phila. 1: 371. 1818. Type: *T. frutescens* (L.) Ell., based on *Glycine frutescens* L.

Wisteria Nutt. Gen. 2: 115. 1818. Type: *W. speciosa* Nutt., based on *Glycine frutescens* L. Sprengel (Syst. 3: 255. 1826) corrected the spelling of the name to *Wistaria*, as the genus had been dedicated to Dr. Wistar.

The genus consists of 5 or 6 species, of which two are native of eastern and southern United States. It is evidently very closely related to the large Asiatic genus *Millettia*, the species of which are mostly trees or shrubs; only a few of them are climbing.

SUBTRIBE 3. BRONGNIARTIANAE

Trees or shrubs, with alternate odd-pinnate leaves, stipules, and sometimes stipels. The flowers are axillary or in terminal racemes or panicles. The calyx is more or less 2-lipped, the tube short, the upper 2 lobes united high up, the lower 3 lobes also somewhat united. The corolla has a broad banner. The stamens are monadelphous or diadelphous. The pod is usually elongate, flat, 2-valved, several-seeded. The seeds are erect, *i.e.*, the longer axis of the seed is at right angles to the axis of the pod, with a well developed strophiole.

The subtribe consists of the following two genera and two from Australia. It is distinguished by the well developed strophiole. Its relationship is probably with the Robinianae.

- | | |
|--|------------------|
| Calyx 5-lobed, the upper 2 lobes united two thirds their length, the lower 3 usually free to near the base; stamens diadelphous. | 5. BRONGNIARTIA. |
| Calyx 2-lipped, the upper 2 and the lower 3 lobes united to the apex; stamens monadelphous. | 6. HARFALYCE. |

5. *Brongniartia* H.B.K. Nov. Gen. & Sp. 6: 465. 1823

Shrubs or trees, with odd-pinnate leaves. Stipules are present, but often caducous, the leaflets entire-margined, sometimes with minute stipels. The flowers are normally axillary in small 1-7-flowered clusters. In some species, however, the upper floral leaves are reduced to the two stipules, which resemble a pair of bracts, and the inflorescence becomes falsely racemose. The individual flowers are subtended by a pair of bractlets, sometimes foliaceous, sometimes reduced to a pair of hair-tufts. The upper two calyx-lobes are united high up, the lower only slightly at the base. The corolla is red, brown, or purple; the banner is broad, its blade orbicular or broadly obovate, short-clawed; the wings are obliquely oblanceolate or obovate, more or less falcate, with a short fleshy claw and a rounded auricle; the blades of the keel-petals are broadly lunate, with a fleshy claw, united from the middle to the tip. The stamens are diadelphous, the alternate ones shorter; the ovary is short-stipitate, the style incurved, glabrous, the stigma minute. The pod is short-stipitate, flat, elongate, 2-valved, usually several-seeded, slightly wing-margined on the upper suture, the valves leathery.

ILLUSTRATION: Plate XXXIV E. *Brongniartia Benthamiana* Hemsl., $\times 2/3$; 1. calyx, 2. staminal sheath, 3. pistil, 4. banner, 5. wing, 6. keel-petals, $\times 1$; 7. pod, $\times 2/3$; 8. seed of *B. sericea* Schlecht., $\times 1$.

The genus was established on two species, *B. mollis* and *B. podalyrioides*, of which the first may be regarded as the type.

Synonyms:

Peraltea H.B.K. Nov. Gen. & Sp. 6: 469. 1823. Type: *P. lupinoides* H.B.K., now known as *Brongniartia lupinoides*.

Megastegia G. Don, Gen. Syst. 2: 468. 1832. Type: *M. speciosa* G. Don, regarded as the same as *B. thermoides*.

The genus consists of 37 species, natives of Mexico and Central America, and a few species from South America. One species, *B. oligosperma* Baill., is somewhat abnormal in the genus on account of its hairy few-seeded pods.

6. *Harpalyce* DC. Mem. Leg. 496. 1825

Trees or shrubs, with alternate odd-pinnate leaves and small stipules. The leaflets are entire-margined, petioluled, sprinkled beneath with yellow or orange glands or gland-like scales. The flowers are racemes. The calyx is 2-lipped, with the upper 2 and the lower 3 lobes united to the tip. The banner is rounded or obovate, short-clawed, the wings are very irregular, strongly curved, obtuse, the keel-petals more or less falcate, united to above the middle but the tips free and obtuse. The stamens are monadelphous, but the sheath is split to the base; the anthers are alternately longer and shorter. The ovary is sessile, the style arcuate, glabrous, the stigma minute, terminal. The pod is 2-valved, several-seeded, leathery or woody.

ILLUSTRATION: Plate XXXIV *F. Harpalyce Loeseneriana* Taub., $\times 2/3$; 1. calyx, 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, $\times 1$; 7. pod, 8. cross section of the same, $\times 1$; 9. banner of *H. cubensis* Griseb., 10. wing, 11. keel-petal, 12. seed, $\times 2/3$.

The genus was based on an unpublished illustration in Mocino and Sesse's Flore de Mexique of *Astragalus carnosus*. In De Candolle's Prodrômus the type is given as *H. formosa* DC., based on the same.

The genus consists of 14 species, viz., 7 from Mexico, 1 from Guatemala, 3 from Cuba, and 3 from Brazil. One species, *H. mexicana*, is abnormal in that the valves of the pod are woody. As the flowers of this species are unknown, it may belong to some other genus. The rest can be divided into three natural groups: (1) Cuban species, in which the petals are fleshy, the keel much longer than the other petals, and the pod is small and narrow; (2) Mexican species (including the one from Guatemala), in which the petals are membranous, the keel is scarcely longer than the banner, and the pod large and broad; (3) Brazilian species, similar to the Mexican but the pod narrower and more or less divided internally by false cross-partitions of spongy tissue.

SUBTRIBE 4. BARBIERIANAE.

Shrubs, with alternate odd-pinnate leaves, narrow stipules and stipels. The flowers are in axillary and terminal racemes, each subtended by a pair of bractlets. The calyx is cylindric, 5-lobed, the lobes subequal. The corolla is not truly papilionaceous, the petals with long slender claws; the blade of the banner is oblanceolate, not spreading; the wings have elliptic blades, the keel-petals oblanceolate or oblong, obtuse blades, scarcely

falcate, and united above the middle. The stamens are diadelphous, the sheath is straight; the ovary is sessile, the style nearly straight to near the apex, hairy along the upper side above; stigma minute. The pod is flat, straight, 2-valved, transversely septate within.

The subtribe consists of a single genus and a single species.

7. *Barbieria* DC. Mem. Leg. 241. 1825

The generic characters are included in the subtribal description.

ILLUSTRATION: Plate XXXIV *G. Barbieria pinnata* (Pers.) Baill., $\times 2/3$; 1. calyx, 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, 7. pod, $\times 1$; 8. cross section of the same; 9. seed, $\times 2$.

The genus was based on *Clitoria polyphylla* Poir. or *Galactia pinnata* Pers. Its distribution extends from Porto Rico to Cuba, southern Mexico, Bolivia, and Brazil.

SUBTRIBE 5. SESBANIANAE

Trees, shrubs, or herbs with abruptly pinnate leaves and caducous stipules but no stipels. The flowers are borne in axillary racemes. The calyx is round-campanulate, fully as broad as high, with very short teeth. The banner has a broad reflexed blade and a short claw; the keel-petals are strongly arcuate, united at the middle, but the claws and tips are free. The stamens are diadelphous; the staminal sheath is dilated below and the upper filament knee-bent near the base. The pod is 2-valved but often indehiscent, stipitate and beaked, compressed, usually with cross-partitions between the seeds, but not disarticulate.

On account of the abruptly pinnate leaves this subtribe, as well as the *Corynellanae*, is somewhat abnormal in the tribe but could not be transferred to the tribe *Vicieae*, to which it does not show any relationship in other ways. The structure of the flower is practically the same as in many genera of the subtribe *Robinianae*; the pod, however, is, in most of the genera, but slightly compressed and internally divided by false transverse partitions.

The subtribe consists of the five following genera, which are thus distinguished.

Pods flattened, neither 4-winged nor 4-angled.

Pods many-seeded, linear, with thick margins; calyx not conspicuously oblique.

Pod not torulose.

Flowers middle-sized or small; banner suborbicular; blades of the broad keel-petals with an auricle; seeds subcylindric-oblong.

8. *SESBAN.*

Flowers large; banner elliptic; blades of the rather narrow keel-petals without a basal auricle; seeds reniform-oblong.

9. *AGATI.*

Pod torulose; banner suborbicular, equaling the other petals; blades of the broad keel-petals without a basal auricle; seeds reniform-oblong.

10. *DAUBENTONIOPSIS.*

Pods 2-seeded, with thin margins, lance-elliptic; seeds oblong-reniform enclosed in the inner membranous layer of the valves; calyx decidedly oblique.

Pod 4-angled, often 4-winged, not torulose.

12. GLOTTIDIUM.

II. DAUBENTONIA.

8. *Sesban* Adans. Fam. 2: 327. 1763

Herbs or shrubs with abruptly pinnate leaves and numerous leaflets. The flowers are borne in axillary racemes, with deciduous bracts, and a pair of deciduous bractlets under the flowers. The corolla is yellow or the banner dotted, streaked, or tinged with purple. The banner has often one or two callosities at the base of the suborbicular reflexed blade; the wings are short-clawed, the blades obliquely oblanceolate or oblong, with a basal auricle; the keel-petals have long claws, the blades are strongly and broadly lunate with a lateral auricle on the upper side. The pod is slender, terete or slightly compressed, short-stipitate, many-seeded, with cross-partitions between the seeds, 2-valved. Seeds cylindro-oblong, subtruncate at the ends.

ILLUSTRATION: Plate XXXIV *H. Sesban Sesban* (L.) Rydb., $\times 1/2$; 1. calyx, 2. stamens, 3. pistil, $\times 2$; 4. banner, 5. wing, 6. keel-petal, $\times 1$; 7. pod, $\times 1/2$; 8. cross section of pod; 9. seed, $\times 2$.

The genus was established on *Aeschynomene Sesban* L. Scopoli (Introd. 308. 1777) changed the name to *Sesbania*, the latter being better Latin form.

Synonyms:

Darwinia Raf. Fl. Ludov. 106. 1817. Type: *D. exaltata* Raf., which has been known under the name *Sesbania macrocarpa* Muhl.

Monaplectra Raf. Fl. Ludov. 106. 1817. This was proposed instead of *Darwinia* in case the latter happened to be preoccupied.

The genus consists of perhaps 20 species of the warmer regions of both hemispheres. It is represented in North America by 4 native and 3 introduced species.

9. *Agati* Adans. Fam. 2: 326. 1763

Small trees, having abruptly pinnate leaves, with many entire leaflets and deciduous stipules. The flowers are large, borne in small axillary racemes, and with two deciduous small bractlets subtending the calyx. The calyx is in structure the same as in *Sesban*. The petals are comparatively narrower, the banner is without callosities, its blade oval in outline, and retuse at the apex; the blades of the wing- and keel-petals are obliquely lanceolate-lunate, tapering at the base without any distinct auricle. The staminal sheath and the pistil resemble also those of *Sesban*, except that they are more gradually arcuate. The pod is the same as in that genus.

ILLUSTRATION: Plate XXXV *I. Agati grandiflora* (L.) Desv., $\times 1/2$; 1. stamens, 2. pistil, 3. banner, 4. wing, 5. keel-petal, $\times 1/2$; 6. pod, $\times 1/4$; 7. cross section of the same, $\times 1$; 8. seed in position in the pod, $\times 1$.

The genus was based on *Robinia grandiflora* L.

Synonym:

Resupinaria Raf. Sylva Tell. 115. 1838. Type: *R. grandiflora* Raf. or *Robinia grandiflora* L.

The genus is represented by *A. grandiflora* (L.) Desv. and one or two species closely related to it and perhaps not specifically distinct from it, natives of southern Asia and northern Australia, and by *A. tomentosa* (H. & A.) Nutt. from the Hawaiian Islands.

10. *Daubentoniopsis* Rydb., gen. nov.

Shrubs, having abruptly pinnate leaves, many entire caducous stipules, caducous bracts and bractlets. The flowers are in axillary racemes. The calyx is rounded campanulate, broader than high, its lobes very short. The corolla is yellow, the banner suborbicular, retuse, reflexed, with a short claw, without callosities; the wings are short-clawed, with obliquely oblong blades, without a distinct basal auricle; the keel-petals are also clawed with a lunate, nearly semicircular blade. The stamens are diadelphous, the staminal sheath dilated at the base. The ovary is stipitate, glabrous, the style arcuate, glabrous; the stigma minute. The pod is coriaceous, stipitate, somewhat compressed, linear, several-seeded, decidedly constricted between the seeds and with spongy transverse partitions. The seeds are oblong-reniform, about twice as long as high.

ILLUSTRATION: Plate XXXV *J. Daubentoniopsis longifolia* (Cav.) Rydb., $\times 1/2$; 1. calyx, $\times 2$; 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, $\times 1$; 7. pod, 8. cross section of the same, $\times 2/3$.

The genus is based on *Aeschynomene longifolia* Cav. Ic. 4: 8. 1797. It is intermediate between *Sesban* and *Daubentonia*, having exactly the flowers and seeds of the latter, but the pod is neither 4-angled nor winged. It is constricted around the seeds, but the exocarp is spongy. In *Sesban* the pod is hardly constricted, the calyx-teeth are more evident, the banner usually has a callosity, and the seeds are different.

The type of the genus, *D. longifolia* (Cav.) Rydb., has a rather peculiar history. It was first described by Cavanilles (*loc. cit.*), and independently by Ortega¹ under the same name. Cavanilles' species was transferred to *Piscidia* by Willdenow.² De Candolle,³ when he established the genus *Daubentonia*, included it in that genus, but from the short description given it is evident that he had in mind a yellow-flowered *Daubentonia* of the southern United States and northern Mexico. In his *Prodromus*⁴ he repeated his error, and besides described on page 265 a *Sesbania longifolia* based on *Aeschynomene longifolia* Ortega. His description fits Cavanilles' plant. When Watson⁵ merged *Daubentonia* into *Sesbania*, he, influenced by De Candolle's misconception, thought himself forced to give the yellow-flowered *Daubentonia* a new name, *S. Cavanillesii* S. Wats., as there was already a *S. longifolia* (Ort.) DC. Unfortunately, however, he based this name on *Aeschynomene longifolia* Cav., and technically he gave a new name

¹ Ort. Dec. 70. 1797-1800.

² Sp. Pl. 3: 920. 1803.

³ Mem. Leg. 286. 1823.

⁴ Prodr. 2: 267. 1825.

⁵ Bibl. Ind. 258. 1878.

to the species of *Daubentoniopsis* instead. Pollard,⁶ following De Candolle's and Watson's interpretation of Cavanilles' plant, was of the opinion that this, being the first one described, should retain the specific name *longifolia*, and therefore proposed the name *S. mexicana* Poll. for Ortega's plant. As the two are the same, he merely added a new synonym to our species of *Daubentoniopsis*. The yellow-flowered *Daubentonia* is still nameless.

11. *Daubentonia* DC. Mem. Leg. 285. 1823

Shrubs or trees, having abruptly pinnate leaves, with many leaflets and deciduous stipules. Flower in axillary racemes, resembling closely those of *Sesban*, but the calyx-lobes are still smaller, the calyx-tube being merely undulate on the margins, slightly ciliate at the teeth. The banner is without callosities, and the wings and keel-petals are without basal auricles. The pod is more or less 4-angled, but somewhat compressed. The endocarp is membranous and constricted around the seeds, the exocarp more or less spongy, the sutures are thick, each produced into two sharp ridges or wings. The seeds are reniform.

ILLUSTRATION: Plate XXXV K. *Daubentonia punicea* (Cav.) DC., $\times 1/2$; 1. calyx, $\times 2$; 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, 7. pod, 8. cross section of the same, $\times 1$.

The type of the genus is *D. punicea* (Cav.) DC., based on *Piscidia punicea* Cav.

The genus consists of about half a dozen species, of which 3 are natives of South America, one of the southern United States and northern Mexico, *Daubentonia Drummondii* Rydb. (*Daubentonia longifolia*? T. & G. Fl. N. Am. 1: 293. 1838), and 1 or 2 of Mexico. I have based it on *D. longifolia*? T. & G., rather than on *D. longifolia* DC., in part as to description, for that name really belongs to *Daubentoniopsis longifolia*, as stated before. One of the South American species, *D. punicea*, has also been found introduced in Florida and Mississippi.

12. *Glottidium* Desv. Jour. Bot. 1: 119. 1813

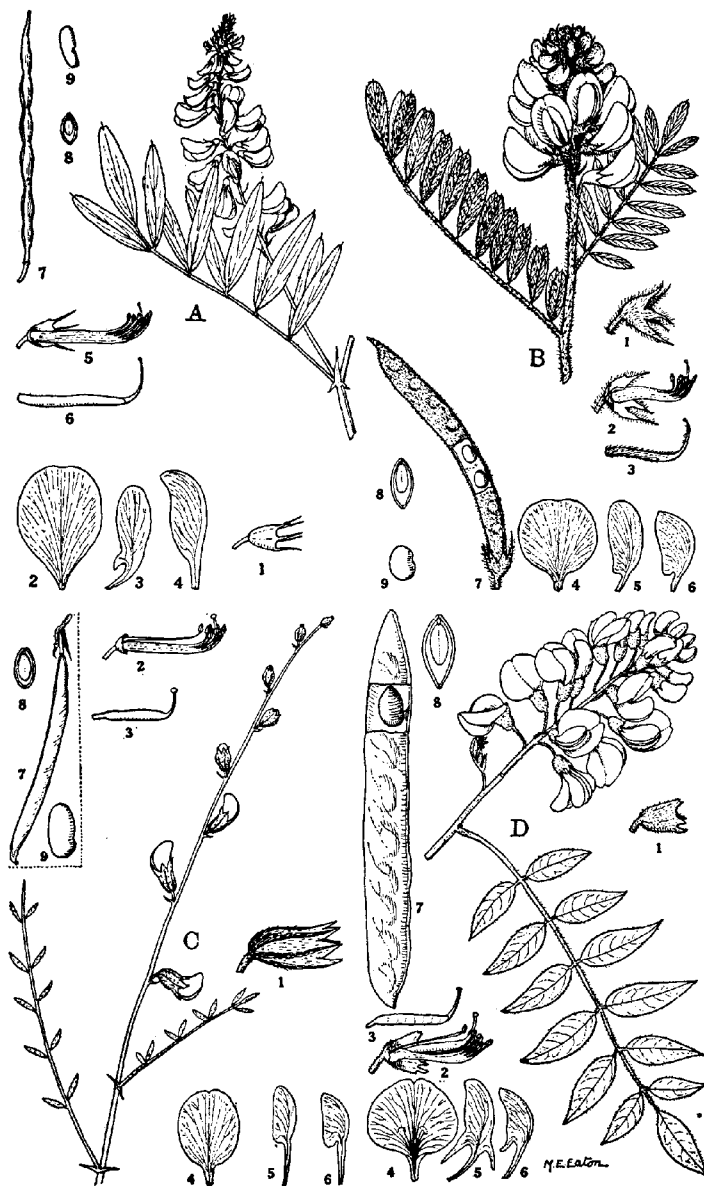
Annual herbs, having abruptly pinnate leaves, with many leaflets and deciduous stipules. The flowers are in axillary racemes or panicles. The calyx and corolla are almost exactly like those of *Sesban*, the banner with callosities, the wings and keel-petals of the same shape as those of that genus. The pod, however, is different, broad, stipitate, compressed, 2-valved, and 2-seeded, the valves at last separating in two layers, the endocarp very thin and papery, the exocarp firmer, somewhat inflated, but not bladderly as in *Diphysa*.

ILLUSTRATION: Plate XXXV L. *Glottidium vesicarium* (Jacq.) Harper, $\times 2/3$; 1. calyx, 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, $\times 2$; 7. pod, $\times 2/3$; 8. pod in cross section, $\times 1$; 9. seed, $\times 2/3$.

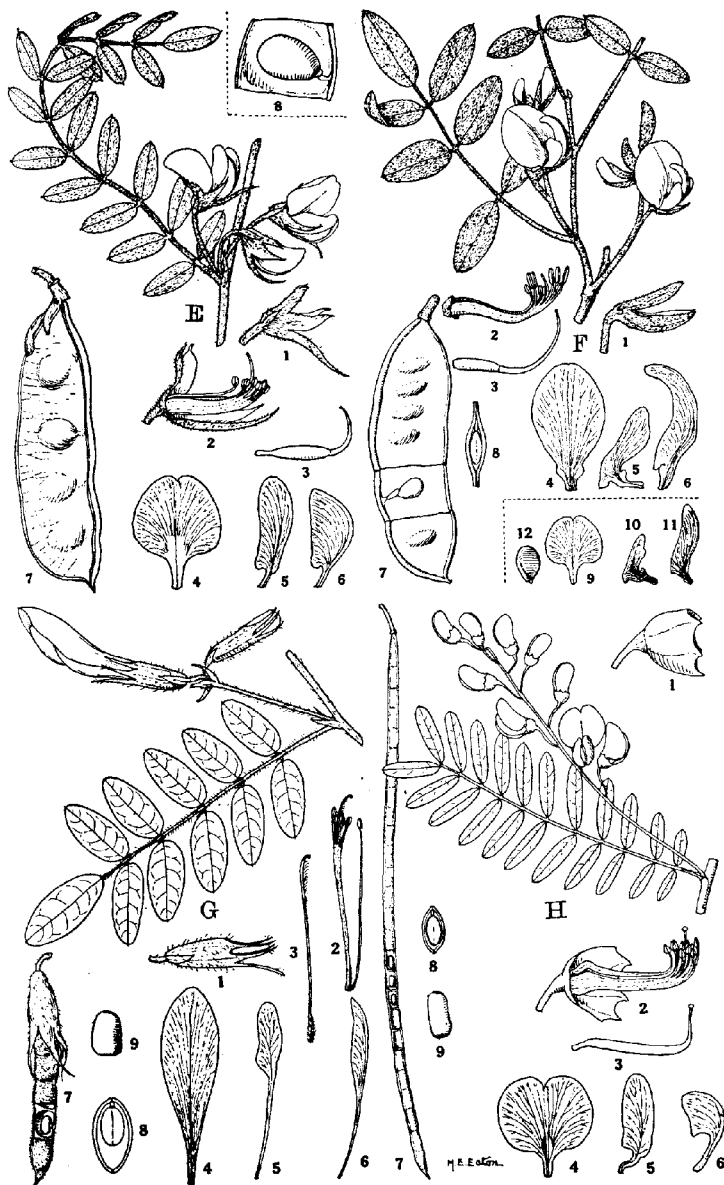
The genus is monotypic and was based on *Aeschynomene platycarpa* Michx., which is the same as *Glottidium vesicarium* (Jacq.) Harper.

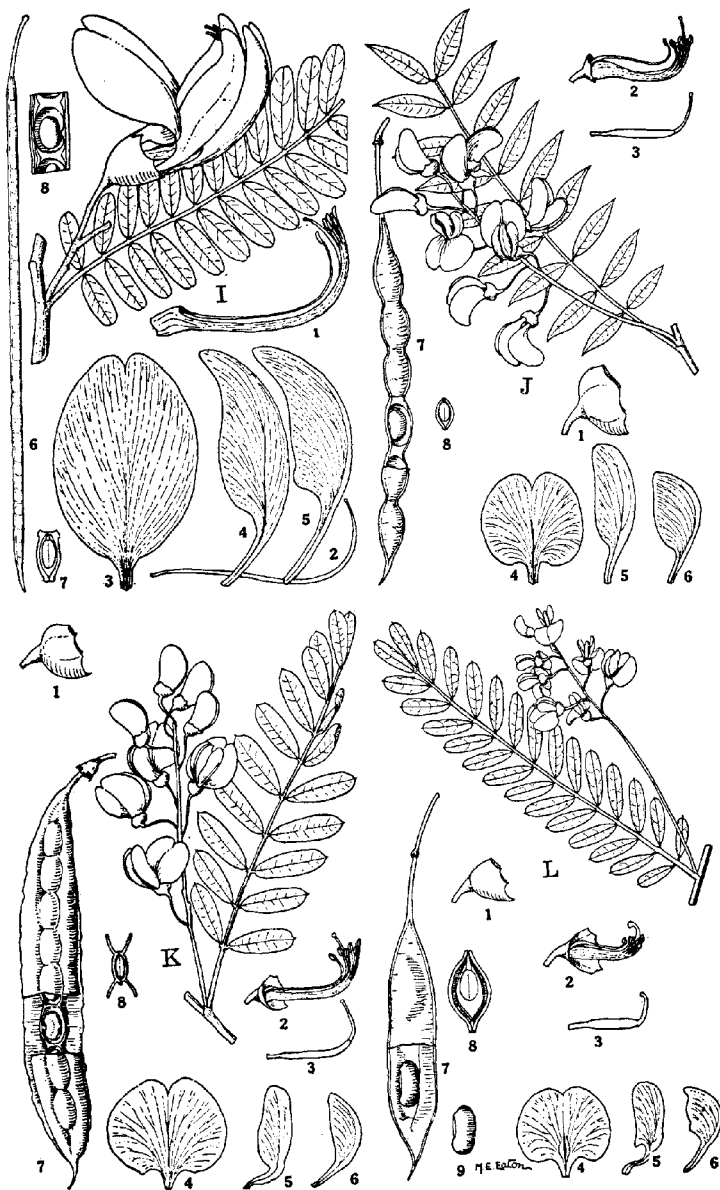
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⁶ Bull. Torrey Bot. Club 24: 154. 1897.



RYDBERG: NORTH AMERICAN FABACEAE





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THE CAMBIUM AND ITS DERIVATIVE TISSUES IV. THE INCREASE IN GIRTH OF THE CAMBIUM

I. W. BAILEY

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INTRODUCTION

Since the publication of Nägeli's (1864) "Dickenwachsthum des Stengels," most botanists, if we may judge from statements in standard textbooks, have assumed that the increase in girth of the lateral meristem, during successive stages in the enlargement of a stem or root, is due to "radial," anticlinal divisions of the cambial initials. Not all investigators, however, have accepted Nägeli's generalization. Robert Hartig (1895) inferred from the structure of the secondary xylem of *Pinus silvestris* L. that the increase in the periphery of the cambium in conifers is due primarily to the elongation of transversely dividing fusiform initials. Klinken (1914) reached a similar inference from the study of serial sections of the phloem of *Taxus baccata* L. He concluded that there are two fundamental types of meristematic activity, one characteristic of the conifers and the other of the dicotyledons. Neeff (1920) subsequently found evidences of Hartig's and Klinken's type of cambial activity in the xylem and phloem of *Tilia tomentosa* which led him to believe that there is no such fundamental distinction between the lateral meristems of gymnosperms and dicotyledons.

There is, of course, a considerable element of uncertainty in ascribing a particular type of meristematic activity to large groups of the vascular plants, either upon the basis of *a priori* deductions or upon that of indirect evidence obtained from the study of the xylem or phloem of one or two supposedly representative species.

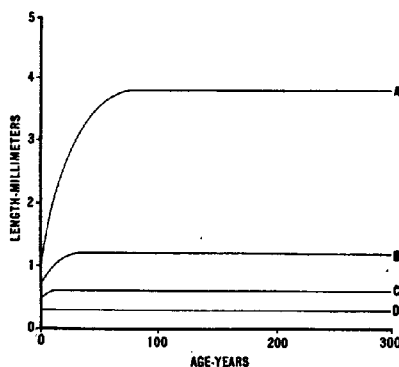
In 1917, the writer perfected methods for sectioning the cambium and for investigating its histological and cytological details. As stated in the third paper (1920 *b*) of this series, he did not succeed in finding evidences of the hypothetical radial, anticlinal divisions which are described and even figured in botanical textbooks. The normal, anticlinal divisions of the fusiform initials, in all of the gymnosperms and less highly specialized dicotyledons examined, were transverse or more or less oblique. That radial longitudinal divisions do occur, at least in certain cases, is suggested however by Kleinmann (1921), upon the basis of the orientation of karyokinetic figures in the cambium of *Raphanus*. In view of these facts, it is evident, on the one hand, that the increase in girth of the lateral meristem is not the simple phenomenon that Nägeli hypothesized, and, on the other

hand, that there may be more than one fundamental type of cambial activity in the vascular plants.

ANALYSIS OF THE PROBLEM

In Nägeli's formulae for computing the frequency of radial divisions, during a given increase in the diameter of a stem or root, the size of the cambial initials is treated as a constant. It is well known, however, that the cambium or lateral meristem is composed of initials of two distinct shapes and sizes: (1) *fusiform initials*, relatively large, elongated elements whose derivatives become differentiated into tracheids, fibers, vessels, sieve tubes, etc.; and (2) *ray initials*, scattered aggregations of small, more or less isodiametric cells which divide to form the horizontal sheets of radially disposed parenchyma, the so-called medullary rays (Plate XXXVI). Therefore, upon the basis of *a priori* considerations, the increase in girth of the lateral meristem might be due to one or more of the following factors:

1. An increase in the tangential diameter of the fusiform initials.
2. An increase in the length of these cells.
3. An increase in the number of these cells.
4. An increase in the diameter of the ray initials.
5. An increase in the number of these cells.



TEXT FIG. 1. Normal curves, showing average lengths of cambial initials at successive stages in the enlargement of a stem. A, Conifer or vesselless dicotyledon. B, Less specialized type of dicotyledon. C, Highly specialized type of dicotyledon. D, Highly specialized type of dicotyledon, having a stratified cambium.

In many of the vascular plants, as the writer has shown in previous papers of this series (1920, 1920a, 1920b), the initials tend to be larger in old stems than in young shoots, but they do not continue to increase in size throughout the entire life of an individual. Thus, in the conifers and

less specialized dicotyledons, where the fluctuations in cell size are considerable, the normal curve of average length of the fusiform initials at successive ages is of the general type illustrated in text figure 1. There is a rapid increase in length for a period of years until a certain size is attained which then remains more or less constant during succeeding growth of the plant. Are these variations in cell size significant factors in the increase in girth of the lateral meristem during the earlier stages in the enlargement of a stem? Some typical measurements taken from *Pinus Strobus* L. are of interest in this connection.

One-year-old stem

Radius of woody cylinder.....	2,000 microns
Circumference of cambium.....	12,566 microns
Average length of fusiform initials.....	870 microns
Average tangential diameter of fusiform initials.....	16 microns
Number of fusiform initials in a cross section of stem.....	724 microns
Average tangential diameter of ray initials.....	14 microns
Number of ray initials in a cross section of stem.....	70 microns

60-year-old stem

Radius of woody cylinder.....	200,000 microns
Circumference of cambium.....	1,256,640 microns
Average length of fusiform initials.....	4,000 microns
Average tangential diameter of fusiform initials.....	42 microns
Average tangential diameter of ray initials.....	17 microns

The increase in width of the original 724 fusiform initials would produce, during the 59-year interval, an arc of 30,408 microns, and the increase in the diameter of the 70 ray initials, during the same interval, an arc of 1,190 microns; or a total circumference of 31,598 microns as compared with the actual circumference of 1,256,640 microns. In other words, the enlargement of the cambial ring, during the 59-year interval, is due primarily to an increase in the number of initials; from 724 to 23,100 fusiform initials and from 70 to 8,796 ray initials.

It is to be emphasized in this connection that such a multiplication of cambial initials—as seen in any given transverse plane or cross section of a stem—is not due necessarily to cell division. For, if the initials elongate and slide by one another, the number which intersect a given transverse plane will be continually augmented. However, if the increase in the number of fusiform initials in *Pinus Strobus* were due entirely to longitudinal sliding growth, the original initials, during the 59-year interval, would have to attain an average length of approximately 26,800 microns instead of 4,000 microns. The ray initials do not elongate to any considerable extent.

In exceptional cases, e.g., *Sequoia*, the fusiform initials may attain a maximum variability in length of 9,000 microns and in width of 60 microns,

but the rate of increase in size during a given period of years is not much in excess of the values recorded for *Pinus Strobus*. Furthermore, the ray initials in certain dicotyledons may have a maximum enlargement in diameter of from 30 to 40 microns, but the variability in the size of their fusiform initials is much less than that which occurs in most conifers.

It is evident, accordingly, that, although the increase in size of the cambial initials, during the earlier stages of the enlargement of certain plants, is by no means a negligible factor, the rapid increase in girth of the lateral meristem must in general be due largely to a progressive increase in the *number*, rather than in the *size*, of its constituent cells.

What then is the relative significance of the increase in the number of the two types of cambial initials? In the young shoot of *Pinus Strobus*, the combined diameters of the 70 ray initials form an arc of 980 microns, whereas those of the 8,796 ray initials in the 60-year-old stem constitute an arc of 149,532 microns, or approximately one eighth of the total circumference of the cambium. Many of the dicotyledons have a much higher percentage of ray initials. Indeed, in extreme cases more than one half of the circumference of the lateral meristem may be occupied by ray initials. Therefore, in discussing the *modus operandi* of the increase in girth of the cambium, it is essential to distinguish between the effects of (1) those anticlinal divisions which are concerned in the origin and multiplication of ray initials, and (2) those which produce an increase in the number of fusiform initials.

The reader should bear in mind in this connection that Nägeli's generalization is based upon the assumption that the divisions in both types of initials are radial, whereas the conclusions of Hartig, Klinken, and Neeff refer to the activity of the fusiform initials. The writer will likewise confine his attention in the following pages to the fusiform initials, reserving further discussion of the ray initials for a subsequent paper of this series.

SIGNIFICANCE OF THE ARRANGEMENT OF FUSIFORM INITIALS

In the gymnosperms and less specialized dicotyledons, the fusiform initials are not arranged in regular rows, whereas in certain of the more highly differentiated dicotyledons they are symmetrically grouped in parallel, horizontal series. The question suggests itself, accordingly, is this striking dissimilarity in the architecture of the lateral meristem indicative of fundamental differences in the growth and division of the fusiform initials, and, if so, what factors are concerned in the transitions from a non-stratified to a stratified arrangement?

As shown in figures 4-6, Plate XXXVI, the "fusiform" initials in stratified meristems are roughly hexangular with long parallel sides and abruptly tapering ends, and the elements of adjacent horizontal series do not overlap to any considerable extent. In other words, the form and the arrangement of the initials indicate very clearly that the increase in girth

of the cambium cannot be due to the *elongation* of transversely dividing cells; for, if it were, the superimposed initials must necessarily crowd by one another and ultimately break up the stratified arrangement. Conversely, if the anticlinal divisions are radio-longitudinal, the products of successive divisions should be grouped in horizontal rows, unless this arrangement is modified by differences in the elongation of adjacent elements. In non-stratified cambia, figures 1-3, the adjacent, overlapping fusiform initials vary considerably in length, but, as the writer has previously stated, the *average length* of these elements does not increase appreciably during the later stages of the enlargement of a stem or root. Thus, the increase in the number of fusiform initials in non-stratified meristems cannot be due solely to radio-longitudinal divisions; for, if it were, there would have to be a general increase in the length of the initials during all stages of the enlargement of the plant.

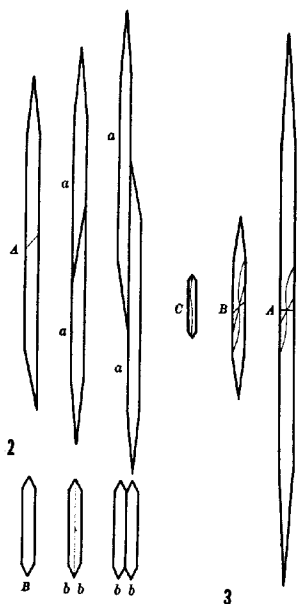
Such facts as these suggest that there are two fundamentally different types of meristematic activity—so far as the fusiform initials are concerned—in the vascular plants; *i.e.*, that the increase in girth of non-stratified cambia is due to the elongation of transversely dividing initials and that of stratified cambia to radio-longitudinal divisions of these elements. Detailed investigations of the cambium and of the histology of its derivative tissues, in numerous representatives of the gymnosperms and dicotyledons, strongly support such an assumption.

The writer has already referred to the fact that in all of the lateral meristems of conifers and less specialized dicotyledons investigated by him—which are, of course, of the non-stratified type—the anticlinal divisions are transverse or oblique (figures 8, 9). The orientation of the cell plates and recently formed anticlinal partitions in the stratified meristems of *Robinia Pseudo-Acacia* L. and of *Diospyros virginiana* L., on the contrary, is radio-longitudinal (figures 6, 7).

Furthermore, since the fusiform initials leave a record of their activities in the xylem and phloem, it is possible to trace successive stages of their growth and division in serial, tangential sections of these tissues.¹ Although this indirect method of studying cambial activity must be applied with a considerable degree of caution, particularly in the case of dicotyledons, it enables one to investigate a large number of plants of which suitable material of the lateral meristem is not readily available. In all of the various genera (62) of gymnosperms and dicotyledons that the writer has examined in this way, the evidence indicates very clearly that the anticlinal divisions in non-stratified meristems are pseudo-transverse, whereas those in stratified cambia are radio-longitudinal. In meristems of the former type, the fusiform initials elongate, sliding by one another, until they attain a certain size. They then divide by means of a more or less oblique partition into*

¹ For detailed descriptions of this method, the reader is referred to Klinken's and Neeff's papers.

two short halves which in turn elongate and divide (text figure 2, *A*). Owing to the fact that the cells do not divide and elongate in unison, there is a very considerable variability in the length of adjacent initials. In addition, owing to the fact that the frequency of the anticlinal divisions and the elongation of the fusiform elements are not constant, the size of the initials tends to fluctuate more or less in different parts of a given individual; e.g., they tend to be considerably shorter in slender shoots than in robust stems (text figure 1). Thus, the non-stratified arrangement and the variability in size of the fusiform cells are both due primarily to elongation



TEXT FIG. 2. Diagrams illustrating *modus operandi* of the increase in girth of cambium in non-stratified and stratified lateral meristems. *A*, Fusiform initial from non-stratified cambium, dividing pseudo-transversely; *a*, *a*, products of this division which elongate and slide by one another. *B*, Fusiform initial from stratified cambium; *b*, *b*, products of the radio-longitudinal division of this initial, which expand laterally but not longitudinally.

TEXT FIG. 3. Types of anticlinal divisions in fusiform initials. *A*, Typical fusiform initial of a conifer. *B*, Fusiform initial of a dicotyledon, having non-stratified cambium. *C*, Fusiform initial of a dicotyledon, having a stratified cambium.

following pseudo-transverse, anticlinal divisions. In meristems of the latter type, on the contrary, the initials divide radio-longitudinally and the products of such divisions expand laterally, but they do not elongate to any considerable extent (text figure 2, *B*). The structure of the secondary

issues in the Calamariales, Sphenophyllales, Lepidophytineae, and Cycadofilices indicates that the cambia in these primitive groups of vascular plants were of the non-stratified type.

In view of these facts, we appear to be justified in concluding that there are at least two distinct, fundamental types of cambial activity in the vascular plants. In the vascular cryptogams, gymnosperms, and less specialized (structurally) dicotyledons, the anticlinal divisions are more or less transverse and the products of these divisions elongate and crowd by one another, producing thereby an increase in the girth of the cambium and a non-stratified arrangement of its cells. In certain of the more highly differentiated dicotyledons, on the other hand, the anticlinal divisions are radio-longitudinal and the products of these divisions expand laterally, thereby increasing the circumference of the cambium, but they do not elongate to any considerable extent, and thus become symmetrically grouped in parallel, horizontal series.

THE TRANSITION FROM THE NON-STRATIFIED TO THE STRATIFIED ARRANGEMENT

In previous papers of this series, the writer (1918, 1920a) has called attention to the fact that in the dicotyledons there is a progressive reduction in the length of the fusiform initials and of their derivatives, which closely parallels successive stages in the differentiation of highly specialized types of vascular tissues. As indicated in table 1, the vesselless dicotyledons (Tetracentron, Trochodendron, and Drimys), whose secondary xylem closely resembles that which occurs in the vascular cryptogams and gymnosperms, have large fusiform initials; fully as large as those of most gymnosperms, for example. Dicotyledons with vessels, on the contrary, are characterized by having much smaller meristematic cells which become shorter and shorter as the tracheary elements become more and more highly specialized. Furthermore, stratified meristems tend, in general, to be composed of smaller fusiform initials than non-stratified cambia. It should be noted, in addition, that, during this sequence of changes, the size-on-age curves (text figure 1) are depressed and ultimately become approximately horizontal; *i.e.*, the length of the fusiform initials is stabilized in plants having stratified meristems.

These facts are of considerable interest in discussing the *modus operandi* of the transitions from one fundamental type of meristematic activity to the other. In most of the non-stratified meristems that the writer has studied, the orientation of the anticlinal partitions fluctuates between a transverse position and varying degrees of obliquity (text figure 3). As the fusiform initials become shorter, the ends of the more oblique partitions tend to approach the extremities of the cells, or, in other words, to become more and more nearly radio-longitudinal. Thus, certain of the more highly differentiated dicotyledons have transitional types of meristems, which show in-

TABLE I. Length (in microns) of adjacent fusiform initials in random samples of the lateral meristem of old stems

NON-STRATIFIED CAMBIA

Gymnosperms

Species	Max. .	Ave.	Min.
<i>Ginkgo biloba</i> L.....	3,000	2,200	1,400
<i>Pinus Strobus</i> L.....	4,000	3,200	2,300
<i>Picea Abies</i> (L.) Karst.....	4,200	3,300	2,400
<i>Juniperus virginiana</i> L.....	3,000	2,200	1,000
<i>Larix decidua</i> Mill.....	5,000	4,000	2,500
<i>Sequoia sempervirens</i> Endl.....	8,700	6,600	4,200
<i>Agathis robusta</i> F. M. Bailey.....	7,700	6,800	4,100
<i>Tsuga canadensis</i> (L.) Carr.....	4,400	3,200	2,200
<i>Podocarpus Nageia</i> R. Br.....	5,000	3,800	2,300
<i>Cedrus libani</i> Barrel.....	4,100	2,900	2,100
Average.....	4,910	3,820	2,450

*Dicotyledons**A. Vesselless*

<i>Trochodendron aralioides</i> Sieb. et Zucc.....	6,200	4,400	2,800
<i>Drimys Winteri</i> Forst.....	4,500	3,300	2,400
Average.....	5,350	3,850	2,600

B. Vascular tissues not highly differentiated

<i>Betula populifolia</i> Marsh.....	1,160	940	700
<i>Myristica philippensis</i> Lam.....	1,620	1,310	990
<i>Altingia excelsa</i> Noronha.....	2,300	1,900	1,200
<i>Liriodendron tulipifera</i> L.....	1,500	1,100	700
<i>Urandra luzoniensis</i> Merr.....	1,700	1,400	1,100
<i>Dillenia philippinensis</i> Rolfe.....	2,300	1,600	1,000
<i>Gordonia Lasianthus</i> L.....	1,700	1,300	1,000
<i>Cornus florida</i> L.....	1,400	1,100	800
<i>Symplocos tinctoria</i> L'Hér.....	1,400	1,100	600
<i>Halesia diptera</i> L.....	1,100	900	800
Average.....	1,620	1,260	890

C. Vascular tissues highly specialized

<i>Carya ovata</i> (Mill.) C. Koch.....	600	520	420
<i>Litsea glutinosa</i> C. R. Rob.....	700	550	390
<i>Prunus serotina</i> Ehrh.....	590	460	320
<i>Excoecaria Agallocha</i> L.....	870	630	410
<i>Mangifera monandra</i> Merr.....	830	570	390
<i>Acer rubrum</i> L.....	610	490	320
<i>Garcentia dulcis</i> Kurz.....	1,020	740	520
<i>Vatica Mangachapo</i> Blanco.....	810	610	410
<i>Barringtonia racemosa</i> (L.) Roxb.....	900	720	500
<i>Psychotria luzoniensis</i> F. Vill.....	1,080	700	450
Average.....	800	600	410

STRATIFIED CAMBIA

*Dicotyledons**D. Vascular tissues highly specialized*

Species	Max.	Ave.	Min.
<i>Grewia multiflora</i> Juss.	370	250	160
<i>Thespesia populnea</i> (L.) Soland. ex Corr.	280	250	210
<i>Bombycidendron Vidalianum</i> Merr. et Rolfe.	430	360	320
<i>Heritiera littoralis</i> Dryand.	360	300	270
<i>Kleinhovia hospita</i> L.	480	360	270
<i>Pterospermum niveum</i> Vid.	430	370	320
<i>Tarrietia sylvatica</i> Merr.	340	280	210
<i>Sterculia foetida</i> L.	450	370	320
<i>Robinia Pseudo-Acacia</i> L.	210	170	140
<i>Diospyros virginiana</i> L.	520	410	320
Average.....	390	310	250

Basis: 50 measurements of fusiform initials.

Probable errors of individual averages 10-15 percent.

ipient stages of stratification. Furthermore, the variability in the size of adjacent fusiform initials in stratified meristems (table 1) is due, at least in part, to the fact that many of the anticlinal divisions are somewhat oblique.²

How much significance should be attached to the close parallelism in the sequences of changes in the cambium and vascular tissues? Is the progressive reduction in cell size in the lateral meristem due to the increasing specialization of the vascular tissues, or *vice versa*? Many morphologists interpret such correlations as due to cause and effect. There is, however, a very considerable element of uncertainty in so doing, where the basis of comparison is time, as Karl Pearson has so clearly shown. Thus, in the absence of reliable collateral evidence it is not possible to determine whether the changes in the cambium are due to those which occur in the vascular tissues or *vice versa*, or whether the parallel sequences are both due to some third factor or group of factors.

SUMMARY AND CONCLUSIONS

1. There are two fundamental types of cambial activity in the vascular plants: one characteristic of the Calamariales, Sphenophyllales, Lepidophytineae, Cycadoflites, Gymnospermae, and less differentiated (structurally) Dicotyledoneae, and the other of certain highly specialized dicotyledons.

2. In the former type the fusiform initials are not arranged in regular rows. The anticlinal divisions are pseudo-transverse and the products of

² The size and the arrangement of the fusiform initials is also modified by the ray initials, new aggregations of which are periodically carved out of the elongated elements.

these divisions elongate and crowd by one another, thereby producing an increase in the girth of the cambium.

3. In the latter type, in which the fusiform initials are relatively short, of nearly uniform length, and more or less symmetrically grouped in parallel, horizontal series, the bulk of the anticlinal divisions is radio-longitudinal, and the increase in the periphery of the cambium is due primarily to the lateral expansion of the products of these divisions.

4. The transition from the non-stratified to the stratified arrangement closely parallels successive stages in the specialization of the vascular tissues, *e.g.*, the differentiation of vessels, libriform fibers, etc., and appears to be due to a progressive reduction of cell size and of longitudinal sliding growth in the cambium.

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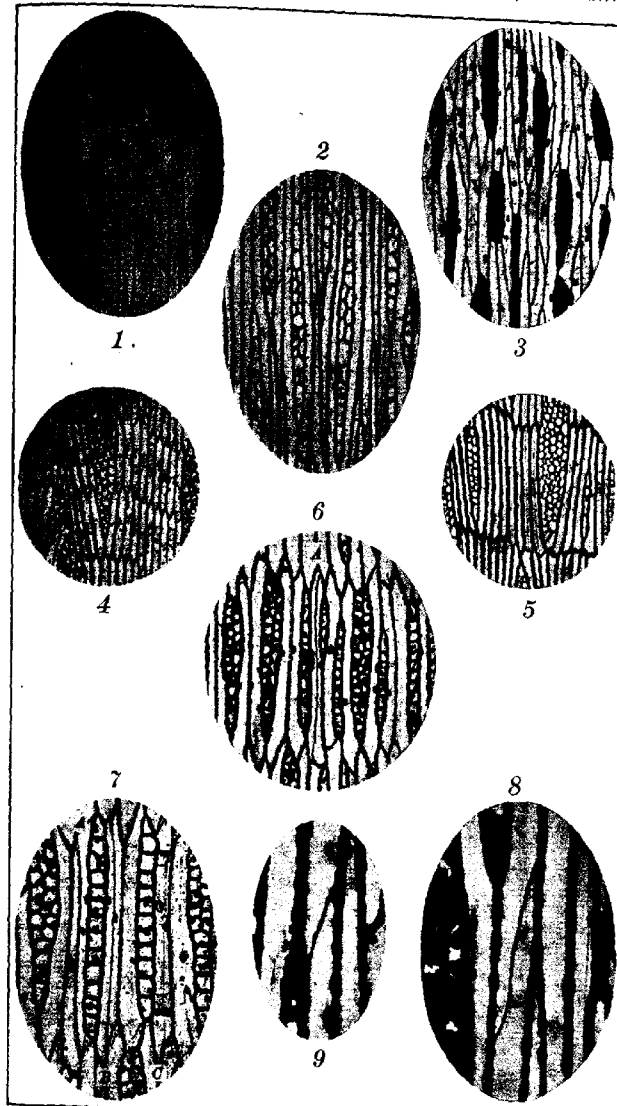
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EXPLANATION OF PLATE XXXVI

FIG. 1. *Pinus Strobus* L. Tangential longitudinal section of non-stratified lateral meristem. The cells are so long that only a portion of each fusiform initial is shown in the photomicrograph. $\times 110$.

FIG. 2. *Myristica philippensis* Lam. Tangential longitudinal section of non-stratified lateral meristem of less highly differentiated type of dicotyledon. $\times 110$.

FIG. 3. *Fraxinus americana* L. Tangential longitudinal section of non-stratified lateral meristem of highly specialized type of dicotyledon. $\times 110$.



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FIG. 4. *Robinia Pseudo-Acacia* L. Tangential longitudinal section of stratified lateral meristem of highly specialized type of dicotyledon, showing parallel horizontal series of fusiform initials. $\times 110$.

FIG. 5. *Heritiera littoralis* Dryand. Tangential longitudinal section of immature phloem, showing stratified elements. $\times 110$.

FIG. 6. *Diospyros virginiana* L. Tangential longitudinal section of stratified lateral meristem. Fusiform initial (A) has divided radio-longitudinally. $\times 110$.

FIG. 7. *Same*. Portion of cambium more highly magnified. Cells A and B have formed radio-longitudinal, anticlinal partitions. Cell C is dividing periclinally. The kinoplasmasomes are approaching the ends of the cell. $\times 148$.

FIG. 8. *Liquidambar Styraciflua* L. Tangential longitudinal section of non-stratified lateral meristem, showing oblique anticlinal division of fusiform initial. $\times 450$.

FIG. 9. *Same*. Oblique anticlinal division. $\times 450$.

TYPE SPECIES OF THE FIRST 100 GENERA OF LINNAEUS' SPECIES PLANTARUM

A. S. HITCHCOCK

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The type concept is finding increasing favor with botanists everywhere. So far as its application to future cases is concerned it may be regarded as already accepted. But when it comes to applying the principle retroactively there is some hesitation on the part of many. Because of the way in which it has been applied by some of the adherents of the American Code, there has been a fear that many well-established names might be superseded if the method were generally used. The rules of the Type-basis Code are more elastic than those of the American Code and would permit a reasonable application of the principle without introducing unnecessary confusion. In my account of the Genera of the Grasses of the United States¹ I typified about 300 genera of grasses according to the rules set forth in the Type-basis Code. In order to test the effect of applying these rules to other genera of flowering plants, I have tentatively typified the first 100 genera of Linnaeus' Species Plantarum. The results are here set forth and analyzed.

Of the 100 genera, 28 contain a single species. These are the types of the respective genera according to any set of rules. Most botanists agree that a generic name should be applied so as to include its original species when there is only one, and one of its original species where there are more than one. However, there are a few cases in which the historic development has followed a different course. An application of the type concept may here cause a profound dislocation of names if a large number of species are involved. Such cases should be considered on their merits and exceptions made if it seems worth while and if a general agreement can be reached.

Among the genera mentioned (often called monotypic genera), there are two cases in which the original species is not included in the genus as now generally accepted. Since the original species is in each case the type, an application of the type concept necessitates a readjustment of the nomenclature of each group. *Alpinia racemosa*, the single species of *Alpinia*, is now referred to *Renealmia*, though the genus *Alpinia*, containing a large number of species, is recognized as valid. Dr. E. D. Merrill has called attention to this case. Among the genera of group I there is one other case of this kind, *Eranthemum capense*, referred to *Daedalacanthus*, though the genus *Eranthemum* with many species is accepted as valid.

¹ U. S. Dept. Agr. Bull. 772. 1920.

The remaining 72 genera, containing originally more than one species, must be typified by selecting one of the species as the type. It is this retroactive application of the type concept that has aroused the most opposition from the adherents of the International Rules because of the fear that well-established names would be needlessly displaced. I think I can demonstrate that the results are not revolutionary and that in the main the fears are groundless. A uniform application of any set of rules will bring to light certain anomalous cases which in some way should be considered and either corrected or validated.

One of the first things to do in selecting a type is to exclude from consideration those species that definitely disagree with the generic description, because certainly an author would not illustrate or typify his own genus with an anomalous species. As there are no generic descriptions in the *Species Plantarum*, the descriptions in the fifth edition of the *Genera Plantarum* (1754) are used to ascertain Linnaeus' concept of the genera included in the *Species Plantarum*. The typification on the basis of the generic description should be done only by those familiar with the taxonomy of the groups. I have not attempted to do this except with the grass genera. As an illustration, we have the genus *Holcus* which does not occur in the first 100 genera now under consideration. The generic description in the *Genera Plantarum* certainly applies only to three of the seven species included in the *Species Plantarum*, the three species related to *Holcus* *Sorghum* which were later segregated as the genus *Sorghum*. The application of the type method here goes contrary to historical development subsequent to Linnaeus and to the general usage of those who recognize the group as distinct from *Andropogon*. In current usage the genus is represented by *Holcus lanatus*.

It is rather exceptional among Linnaean genera to find species definitely excluded in this way from consideration in selecting the type. It is possible that on taxonomic grounds there may be a few changes in the tentative list of type species here presented.

The next point to ascertain is which species the author of the genus appeared to have chiefly in mind, in so far as one species can be singled out. We may assume, unless there is evidence to the contrary, that the representative species to the author would be the one best known to him. This may be shown in four ways: First, one to which he has applied a specific name like *officinalis*, *communis*, *vulgaris*, or *sativus*; second, a well-known economic species; third, a common species of the native flora or one grown by him in a garden; fourth, through a citation in the *Genera Plantarum*. Another method, the selection on the basis of figures accompanying the original description, can not be used here because there are no plates in the *Species Plantarum*. These four methods are used coordinately. Sometimes one can be applied, sometimes another. Often two or more methods lead in the same direction, as in *Hordeum*, of which *H. vulgare* is selected as the

type on the basis of its being an economic species. But it would be indicated as the type through the name *vulgare* and through the Tournefort figure cited in the Genera Plantarum. If different methods conflict, the factors must be considered and a balance struck. In the list submitted there appears to be no conflict except in *Justicia* which is considered separately.

In selecting a native species one assumes that a European species will be better known to Linnaeus than one from some other continent; that a Swedish species would be better known than one from southern Europe; and that one grown in the Hortus Cliffortianus or Hortus Upsaliensis better known than one represented by a herbarium specimen only. One should select a species on the basis of a figure cited in the Genera Plantarum only when there is no doubt as to the identity of the figure, and the method should be used with caution.

After these four methods have been applied there are still some cases in which a selection has not resulted. At this point the historical development should be considered. In these genera, amounting to about 20 percent in our list, the type has been chosen from among the original species now commonly retained in the genus, thus fixing the application of the generic name in accord with current usage.

In case there are more than one residual species, the type is the most common or best known, or, if equally eligible, the first of these.

Among the 72 genera considered there are a few that must receive attention separately.

Justicia contains 9 species of which four are retained in the genus under present usage. The first of these is *J. betonica*. The citation in the Genera Plantarum refers to *J. sexangularis*, which is now usually placed in *Dicliptera*. The selection of this species as the type would change the application of *Justicia* as currently understood. If the citation in the Genera Plantarum is ignored, the type is *J. betonica* and the genus falls in group 5.

Ixia contains two species, both of which are now referred to later genera, *I. africana* to *Aristaea*, *I. chinensis* to *Belamcanda*. On the type basis one of these species, probably the first, should be accepted as the type, and the nomenclature of the other groups adjusted accordingly.

Minuartia contains 3 species, all of which are currently referred to *Alsine*.² The nomenclature of this group has been considered by Sprague and others. The three species, all from Spain, appear to be equally eligible for the type, and the first, *M. dichotoma*, may be selected.

Aira contains 14 species of which four were included in the first use of the name in the Flora Lapponica. The type would ordinarily be chosen

²In the original issue of the Species Plantarum, *Minuartia* appears with a single species, *M. hispanica*. This leaf (pages 89 and 90) was reprinted and inserted in place of the original. A very few copies escaped the correction. An account of the insertion of the corrections is given in Bot. Centralbl. 66: 216. 1896, 67: 5. 1896, and Jour. Bot. 34: 359. 1896. The photographic reprint of the work was made from the original issue.

from these four as they represent Linnaeus' original concept of the genus and there is nothing to show that the concept was altered in the *Species Plantarum*, except by enlargement. Of these four, one, *A. spicata*, is now referred to *Trisetum*. In my account of the Genera of Grasses I selected *A. caespitosa* as the type. The historic development was different. The last-mentioned species was taken out as the type of *Deschampsia* and the other species were referred to other genera, leaving in *Aira*, as commonly accepted, only *A. praecox* and *A. caryophyllea*, species not found in the *Flora Lapponica*. In this case my application of the type method gives a result contrary to current usage.

Leucadendron contains 13 original species, and *Protea* contains two. In the *Index Kewensis* all the original species of *Leucadendron* are referred to *Protea*, and the two species of *Protea* are referred to *Leucadendron*. Both genera are accepted as valid, but neither, as accepted, contains any of its original species. An application of the type method will seriously disturb two large genera. *Leucadendron* and *Protea* are included in the list of conserved names of the International Rules.

The purpose has been to show that the rules as given in the Type-basis Code for the typification of genera when concretely applied do not result in any startling upheaval of nomenclature or radical changes in the application of generic names. The few cases mentioned at the end, only six percent of the list, would require special attention under any set of rules.

The 72 genera in which there are more than one original species are grouped below, each with its type species as selected according to the method outlined. The first four groups are coördinate and the sequence has no significance.

Group 1. Specific name *officinalis*, *vulgaris*, *communis*, or *sativus*.

<i>Jasminum officinale</i>	<i>Verbena officinalis</i>
<i>Syringa vulgaris</i>	<i>Salvia officinalis</i>
<i>Veronica officinalis</i>	<i>Valeriana officinalis</i>
<i>Gratiola officinalis</i>	<i>Crocus sativus</i>
<i>Pinguicula vulgaris</i>	<i>Gladiolus communis</i>
<i>Utricularia vulgaris</i>	<i>Commelina communis</i>

Group 2. The type an economic species.

<i>Piper nigrum</i>	<i>Dactylis glomerata</i>
<i>Saccharum officinarum</i>	<i>Avena sativa</i>
<i>Panicum miliaceum</i>	<i>Lolium perenne</i>
<i>Phleum pratense</i>	<i>Secale cereale</i>
<i>Alopecurus pratensis</i>	<i>Hordeum vulgare</i>
<i>Agrostis stolonifera</i>	<i>Triticum aestivum</i> ³
<i>Poa pratensis</i>	

³ *Triticum aestivum* and *T. hybernum* are equally eligible.

Group 3. Type the commonest or best-known species.

<i>Kaempferā galanga</i>	<i>Cynosurus cristatus</i>
<i>Boerhavia diffusa</i>	<i>Festuca ovina</i>
<i>Salicornia europaea</i>	<i>Elymus sibiricus</i>
<i>Olea europaea</i>	<i>Halosteum umbellatum</i>
<i>Lycopus europaeus</i>	<i>Mollugo verticillata</i>
<i>Milium effusum</i>	<i>Queria hispanica</i>
<i>Melica nutans</i>	<i>Blitum capitatum</i>
<i>Briza media</i>	

Group 4. Type based on the citation in the Genera Plantarum.

<i>Canna indica</i>	<i>Scirpus lacustris</i>
<i>Phyllirea latifolia</i>	<i>Bromus secalinus</i>
<i>Iris germanica</i>	<i>Eriocaulon decangulare</i>
<i>Cyperus rotundus</i>	

Group 5. One of the residual species.

<i>Amomum cardamon</i>	<i>Schoenus nigricans</i>
<i>Curcuma longa</i>	<i>Eriophorum vaginatum</i>
<i>Corispermum hyssopifolium</i>	<i>Nardus stricta</i>
<i>Nyctanthes arbor-tristis</i>	<i>Phalaris canariensis</i>
<i>Chionanthus virginicus</i>	<i>Uniola paniculata</i>
<i>Circaea lutea</i>	<i>Lechea minor</i>
<i>Zizophora capitata</i>	<i>Cephalanthus occidentalis</i>
<i>Monarda fistulosa</i>	<i>Stipa pennata</i>
<i>Anthoxanthum odoratum</i>	<i>Arundo donax</i>
<i>Antholyza cunonia</i>	

SUMMARY

Genera with a single original species.....	28
Genera with more than one original species.....	72
Group 1. Type based on specific name.....	12
Group 2. Type an economic species.....	13
Group 3. Type a well-known species.....	15
Group 4. Type based on citation in Genera Plantarum.....	7
Group 5. Type a residual species.....	19
Special cases.....	6
Total.....	100

BUREAU OF PLANT INDUSTRY,
WASHINGTON, D. C.